PHYLOGENY OF THE CICHLID SUBFAMILY ETROPLINAE AND TAXONOMIC REVISION OF THE MALAGASY CICHLID GENUS *PARETROPLUS* (TELEOSTEI: CICHLIDAE)

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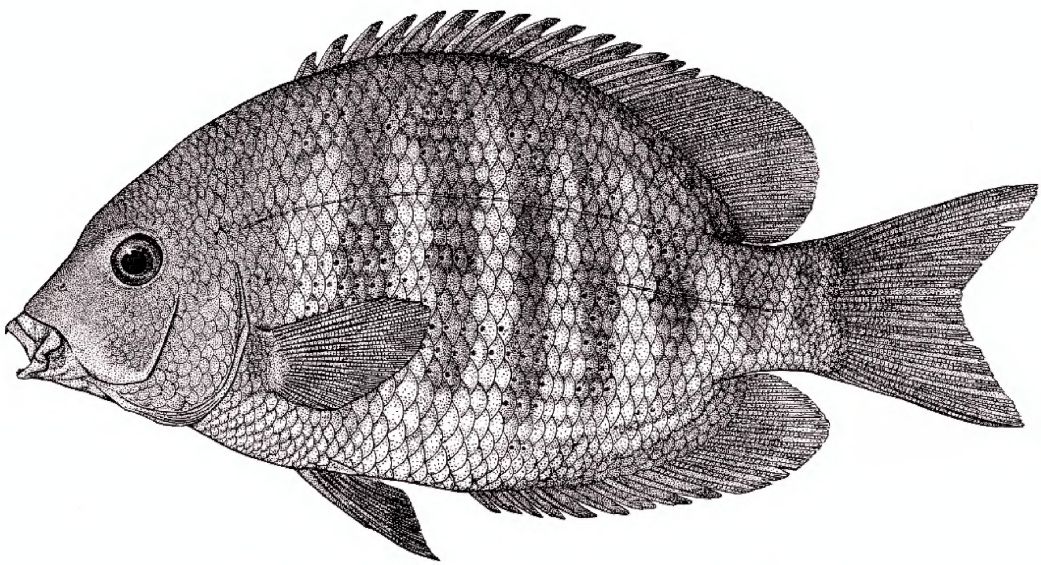

Holotype of *Paretroplus maromandia*, UMMZ 234790.
Drawing by T. L. Peterson modified from Sparks and Reinthal, 1999.

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ABSTRACT

A species-level phylogeny for Etroplinae is presented, based on the simultaneous analysis of morphological and nucleotide characters, and species of the endemic Malagasy genus *Paretroplus* are taxonomically revised, including the description of two new species. Relative to most other cichlid genera, *Paretroplus* is diagnosed by numerous anatomical features, including morphology of the gas bladder, neurocranium, oral jaws and dentition, and suspensorium. Keys to the genera of Malagasy–South Asian cichlids and to the species of *Paretroplus* are provided. *Paretroplus* is endemic to Madagascar and is the sister genus to *Etroplus*, endemic to southern India and Sri Lanka. Together these two genera comprise the subfamily Etroplinae. *Paretroplus* comprises 12 species, two of which are described herein as new. Three morphologically distinct clades are recovered within *Paretroplus*, one comprising the comparatively elongate, primarily riverine and rheophilic species *P. damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, new species, the second comprising the deep-bodied, primarily lacustrine species *P. polyactis*, *P. petiti*, *P. kieneri*, *P. maculatus*, *P. menarambo*, *P. maromandia*, and *P. dambabe*, and the third comprising the shallow-bodied and highly mottled species *P. kieneri* and *P. gymnopreopercularis*, new species, which occur in both lentic and lotic habitats. Monophyly of Etroplinae and *Etroplus* are also discussed and diagnostic anatomical features are presented for both clades. The sister-group relationship between *Etroplus* and *Paretroplus* represents a well-corroborated transoceanic link within Cichlidae, a pattern congruent with the Mesozoic fragmentation of Gondwana. The anterior of the gas bladder is highly modified in Etroplinae, reaching its most derived configuration in *Paretroplus*, in which multiple, structurally complex and rigid anterior bullae expand into large exoccipital recesses, forming a mechanical (= otophysic) connection between the gas bladder and inner ear. Evolution of the gas bladder, and its function in conferring increased hearing ability, is discussed in terms of the phylogenetic information this structure provides for reconstructing hypotheses of relationships within Cichlidae.

INTRODUCTION

Etroplinae, following Sparks (2004a) and Sparks and Smith (2004), is a highly anatomically modified clade of cichlid fishes, and comprises *Etroplus* Cuvier, in Cuvier and Valenciennes, 1830 (three spp.), endemic to southern India and Sri Lanka, and *Paretroplus* Bleeker, 1868 (12 spp.), endemic to eastern and northwestern Madagascar. Etroplinae is recovered as the sister group to the remainder of Cichlidae (Sparks and Smith, 2004: fig. 1). Although separated by the Indian Ocean, due to striking similarities in external morphology *Etroplus* and *Paretroplus* have been hypothesized to have a sister-group relationship since the original description of *Paretroplus* by Bleeker (1868) to encompass his newly described species *P. damii*. This trans–Indian Ocean relationship has been widely accepted by subsequent workers including Regan (1920), Cichocki (1976), and Stiassny (1991). Whereas numerous morphological features unite *Etroplus* and *Paretroplus*, several apomorphic features, nevertheless, are diagnostic of each genus (Sparks, 2001; Stiassny et al., 2001; Sparks and Smith, 2004; this study). Cichocki (1976), who examined a number of specimens from each genus for his family-level phylogenetic analysis, concluded that *Paretroplus* was probably not distinct enough to warrant generic status, a statement with which I strongly disagree and which is refuted by the evidence presented herein.

Paretroplus and *Etroplus* differ substantially, for example, with regard to modifications to the anterior of the gas bladder and posterior neurocranium. Paired anterior gas bladder extensions are found in all members of Etroplinae and are firmly lodged in and expanded within characteristic exoccipital foramina, such that they form a direct mechanical (= otophysic) linkage between the gas bladder and inner ear. In *Paretroplus* these structures are highly modified, and the multiple anterior polyplike chambers or bullae that characterize the genus exhibit a tough and thickened tunica externa, with extremely narrow connections (diverticula) to the main gas bladder chamber. In *Etroplus*, however, the anterior bullae are rather

typical broad, tubelike extensions with a feeble tunica externa, although they too are firmly lodged in large exoccipital foramina.

A number of corresponding modifications of structures that presumably convey enhanced hearing ability (e.g., large and complex exoccipital foramina, excavation of the posterior margin of the supraoccipital crest [pronounced in *Paretroplus* that inhabit lacustrine environments], the presence of a supraoccipital-exoccipital prong, modifications and enlargement of the foramen magnum, and enlarged and expanded anterior neural arches) also characterize members of *Paretroplus* (Sparks, 2001; Stiassny et al., 2001). It should be noted, however, that Cichocki (1976) did not compare these anatomical character complexes. Herein, 31 unambiguously optimized morphological features are presented that diagnose *Paretroplus*, 28 of which are unique and unreversed.

Paretroplus are medium-sized to large cichlid fishes found in a variety of habitats, including rivers, shallow floodplain lakes, and brackish and marshy coastal environments throughout northwestern and eastern coastal Madagascar (Sparks, 2001, 2002a, 2004a; de Rham and Nourissat, 2004). *Paretroplus* are absent from central western, central highland, and southwestern drainages. Generally, species of *Paretroplus* exhibit highly allopatric distributions. *Paretroplus kieneri,* which exhibits a relatively wide distribution, is exceptional within the genus in that this species is usually found in sympatry with another member of the genus (see Species Accounts). Their greatest diversity is concentrated in the northwestern part of the island, where 11 species occur, whereas only a single taxon, *P. polyactis*, is restricted to eastern drainages. *Paretroplus damii* is the only member of the genus that occurs in both eastern and western basins (P. Loiselle, personal commun.; de Rham and Nourissat, 2004). Certain species within this assemblage (e.g., *P. polyactis* and *P. maromandia*) exhibit tolerance to brackish or saline environments and may be found, temporarily at least, in full seawater (J. Sparks, personal obs.). All members of the genus are highly threatened (with the possible exception of *P. polyactis*) due to habitat destruction, overfishing, and competition from a number of exotic species (primarily tilapiine cichlids and the Asian snakehead). Until very recently, when a small isolated population was discovered, one species, *P. menarambo* Allgayer 1996, was presumed extinct. Based on recent surveys, *P. dambabe* Sparks, 2002 and *P. petiti* Pellegrin, 1929 may also be extinct in the wild.

In the current study, a phylogenetic analysis of Etroplinae is presented, and *Paretroplus* is taxonomically revised based on the hypothesis of relationships recovered using a combination of morphological features and nucleotide characters. This revision is timely in light of the description of several species of *Paretroplus* new to science (Allgayer, 1996, 1998; Sparks and Reinthal, 1999; Sparks, 2002a; Stiassny et al., 2001) within the last decade. Although a few works to date have included a summary of species of *Paretroplus* known at the time (Pellegrin, 1904, 1933; Kiener and Maugé, 1966), a formal revision of the genus has never been undertaken. Kiener and Maugé (1966) presented a descriptive study of the Malagasy cichlids in which they illustrated anatomical features of the oral and pharyngeal jaws for *Paretroplus*. They presented a key to the five species of *Paretroplus* known at that time, including a new species, *P. maculatus*, described in that study, but did not attempt to resolve relationships among members of the genus. With the subsequent description of several novel species (Allgayer, 1996, 1998; Sparks and Reinthal, 1999; Stiassny et al., 2001; Sparks, 2002a), the aforementioned studies are now quite incomplete and outdated. A cladistic analysis of *Paretroplus* based on morphological features has yet to be published, although two recent studies have resolved relationships within the genus using nucleotide characters (Sparks, 2004a; Sparks and Smith, 2004). In the current study, monophyly of *Paretroplus*, *Etroplus*, and an assemblage comprising both genera (subfamily Etroplinae) is tested using a combination of anatomical and nucleotide characters.

This taxonomic revision of *Paretroplus* is undertaken in the context of a robust phylogenetic hypothesis. The importance of undertaking taxonomic revisions within a phylogenetic context cannot be overstated, although few revisions are, in reality, based

on robust species-level phylogenetic hypotheses. As a result most taxonomic revisions are merely authoritative descriptive studies that lack any hierarchical structure. Moreover, contrary to the claims of many authors of such studies, the hypotheses of relationships presented are not derived via a formal analysis of characters. Sparks and Reinthal (1999), Sparks (2002a), and Stiassny et al. (2001) placed their newly described species of *Paretroplus* within a phylogenetic framework (i.e., diagnosing subclades within *Paretroplus* to encompass these new species). Here, the phylogenetic analysis precedes the taxonomic revision, such that under the individual species accounts, taxa can be discussed in their proper phylogenetic context and with reference to their sister taxa. It should also be noted that certain subclades within *Paretroplus*, recovered in studies based on molecular evidence (Sparks, 2004a; Sparks and Smith, 2004), are not currently diagnosable based on apomorphic morphological features. The purpose of this paper is to present a species-level phylogeny for the etropline cichlids based on the combined analysis of morphological and molecular evidence, diagnose Etroplinae, *Etroplus*, and *Paretroplus* on the basis of derived anatomical features, and to present redescriptions and diagnoses for all nominal species of *Paretroplus*, including the description of two new species of *Paretroplus*.

MATERIALS AND METHODS

Morphology: Counts and Measurements

Counts and morphometric measurements follow Barel et al. (1977), Kullander (1986) for upper jaw length and pelvic fin length, and Sparks and Reinthal (1999, 2001) and Sparks (2002a) for gill raker and vertebral counts unless noted otherwise. Measurements were verified at least twice and recorded to the nearest 0.1 mm using digital or dial calipers. Vertebral counts exclude the terminal, hypural-bearing vertebra (i.e., last half centrum). Vertebral and fin spine/ray counts and measurements were obtained from radiographs or cleared-and-stained (C&S) preparations. The terminal dorsal- and anal-fin soft rays are counted as a single element, even if branched and split to the fin base, as this element is associated with a single supporting pterygiophore. Lateral line scales were counted following the method of Greenwood (1956), and include scales in the lower branch up to the hypural flexure (i.e., a vertical through the caudal border of the hypurals). Pored scales posterior of the hypural flexion are excluded from the count, regardless of size. Osteological characters of the new species and related taxa were examined using alcoholic specimens, cleared-and-stained (C&S) and dry skeletal preparations (S), or obtained from radiographs. In the list of material examined (appendix 1), the designations "C&S" and "S" indicate that these wet and dry skeletal preparations, respectively, were examined for the corresponding specimens. Gill raker counts (lower limb of the first gill arch, including rakers associated with both hypobranchial and ceratobranchial) exclude the raker in the angle of the arch marking the transition from ceratobranchial to epibranchial.

Morphology: Taxon Sampling and Characters

In the course of this study all nominal species of Malagasy–South Asian cichlids have been examined, as well as putatively novel and undescribed Malagasy cichlid species, and a number of cichlid and noncichlid outgroup taxa (appendix 1). Materials included in comparative analyses represented formalin-fixed specimens preserved in 70% ethanol, dry skeletal preparations (S), and specimens cleared-and-stained (C&S) for bone and cartilage using a modified protocol based on Pothoff (1984) and Taylor and Van Dyke (1985). When sufficient material was available at least two specimens were cleared and stained and dissected for each species. Cleared-and-stained individuals were examined from all species of *Paretroplus* except *P. petiti*, for which only the formalin-fixed holotype is known. Dissections were made according to a standard protocol for small teleosts (Weitzman, 1974). Drawings were made using a dissecting microscope equipped with a camera lucida, and edited using Adobe Illustrator (vers. CS2) or Adobe Photoshop (vers. CS2). All drawings were made from the

left side of the specimens unless noted otherwise.

Morphological characters utilized in this study are either novel or were obtained (and frequently modified) from descriptions in Cichocki (1976), Oliver (1984), Stiassny (1981, 1990, 1991), Reinthal and Stiassny (1997), Sparks and Reinthal (1999, 2001), Sparks (2001, 2002a, 2002b, 2003, 2004a, 2004b), Stiassny et al. (2001), and Stiassny and Sparks (2006). The morphological character matrix used in the phylogenetic analysis is presented in appendix 2. Terminology of bones, joints, and ligaments in the head in general follows Barel et al. (1976, 1977), Greenwood (1985), and Anker (1986, 1987, 1989). In the course of this investigation, all characters from the literature that are incorporated into this analysis have been reexamined and verified. Many characters reported in earlier studies have been modified or redefined from their original source. When necessary, figures from the works of the authors cited above are referenced. Citations presented with the character descriptions identify the relevant character source(s). Under comparative material, the total number of specimens examined from each lot is listed (and does not necessarily correspond to the total number of individuals in the lot, but only those available for study), followed by the number of wet (C&S) or dry (S) skeletal preparations examined from within that total. Specimens used in comparative morphological analyses are deposited at the following institutions (abbreviations follow Leviton et al., 1985):

Institutional Abbreviations

AMNH	American Museum of Natural History, New York
BMNH	Natural History Museum, London
CU	Cornell University Museum of Vertebrates, Ithaca
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Cambridge
MHNG	Muséum d'Histoire Naturelle, Genève
MNHN	Museum National d'Histoire Naturelle, Paris
MNRJ	Museo National de Rio de Janeiro, Brasil
MRAC	Musee Royal de l'Afrique Centrale, Tervuren, Belgium
RMNH	Rijksmuseum van Natuurlijke Historie (Nationaal Natuurhistorisch Museum), Leiden
UAZ	University of Arizona, Tucson
UMMZ	Museum of Zoology, University of Michigan, Ann Arbor
USNM	National Museum of Natural History, Washington, D.C.

Phylogenetic Approach and Outgroups

A cladistic approach is adopted herein, and only shared derived character states (= synapomorphies or homologies) are used to diagnose monophyletic groups (Hennig, 1966). The numbered anatomical characters (= morphological transformations) listed below each represent a hypothesized synapomorphy. In order to rigorously test the monophyly of the etropline cichlids (= Etroplinae), *Paretroplus*, and *Etroplus*, as well as reconstruct intrageneric relationships, 82 morphological features were coded for 25 cichlid terminals, including all members of Etroplinae, representatives of all other Malagasy cichlid genera, and representative basal African and Neotropical cichlid lineages (table 1). A data set combining these 82 morphological transformations and nucleotide characters from multiple mitochondrial and nuclear genes was subjected to cladistic analysis under the optimality criterion of parsimony (see Phylogenetic Analyses below). Outgroup choice was based on the results of prior morphological and molecular studies (Sparks, 2001; Sparks, 2004a; Sparks and Smith, 2004). Some recent studies based on nucleotide characters, or a combination of morphological features and nucleotide characters, support monophyly of the Malagasy–South Asian cichlids, albeit weakly, and suggest that either the ptychochromine cichlids inclusive of *Paratilapia* (= Ptychochrominae after Sparks and Smith, 2004), or a member of Ptychochrominae, is the sister group to Etroplinae (Farias et al., 1999, 2001; Sparks, 2001, 2003, 2004a). The most com-

TABLE 1
Collection localities, sources/original citations, and GenBank accession numbers for taxa included in molecular phylogenetic analyses. All of the sequences, except *Heterochromis multidens*, were originally published in Sparks (2004) and Sparks and Smith (2004).

Species	Source	*16S*	*COI*	*Tmo-4C4*	*Histone H3*
Etroplinae – India/Sri Lanka					
Etroplus canarensis	Sparks & Smith, 2004	AY662713	AY662766	AY662816	AY662890
Etroplus suratensis	Sparks, 2004	AY263829	AY263870	AY662817	AY662891
Etroplus maculatus	Sparks, 2004	AY263830	AY263858	AY662818	AY662892
Etroplinae – Madagascar					
Paretroplus dambabe	Sparks, 2004	AY263822	AY263851	AY662819	AY662893
Paretroplus damii	Sparks, 2004	AY263827	AY263856	AY662820	AY662894
Paretroplus kieneri "Kinkony"	Sparks, 2004	AY263827	AY263854	AY662821	AY662895
Paretroplus kieneri "Betsiboka"	Sparks & Smith, 2004	AY263825	AY263855	AY662822	AY662897
Paretroplus gymnopreopercularis n. sp.	Sparks & Smith, 2004	AY662715	AY662768	AY662823	AY662898
Paretroplus maculatus	Sparks, 2004	AY263820	AY263872	AY662824	AY662899
Paretroplus maromandia	Sparks, 2004	AY263821	AY263852	AY662825	AY662900
Paretroplus menarambo	Sparks, 2004	AY263823	AY263853	AY662826	AY662901
Paretroplus nourissati	Sparks, 2004	AY263828	AY263857	AY662827	AY662902
Paretroplus polyactis "South"	Sparks, 2004	AY263826	AY263871	AY662828	AY662903
Paretroplus tsimoly	Sparks & Smith, 2004	AY662716	AY662769	AY662829	AY662904
Paretroplus lamenabe n. sp.	Sparks & Smith, 2004	AY662717	AY662770	AY662830	AY662905
Ptychochrominae – Madagascar					
Oxylapia polli	Sparks, 2004	AY263817	AY263881	AY662832	AY662907
Paratilapia c.f. *bleekeri*	Sparks, 2004	AY263819	AY263885	AY662833	AY662908
Paratilapia polleni "Nosy Be"	Sparks & Smith, 2004	AY662719	AY263886	AY662834	AY662909
Ptychochromoides vondrozo	Sparks, 2004	AY263816	AY263883	AY662839	AY662914
Ptychochromoides katria	Sparks, 2004	AY263814	AY263880	AY662840	AY662915
Ptychochromis grandidieri	Sparks, 2004	AY263811	AY263878	AY662841	AY662916
Ptychochromis oligacanthus "Nosy Be"	Sparks, 2004	AY263813	AY263873	AY662843	AY662918
Cichlinae – Neotropics					
Retroculus xinguensis	Sparks & Smith, 2004	AY662733	AY662784	AY662857	AY662934
Pseudocrenilabrinae – Africa					
Heterochromis multidens	Farias, et al., 1999, 2000	AF048996	Unavailable	AF113060	Unavailable

prehensive and data-rich study of cichlid intrafamilial relationships to date, however, suggests that Etroplinae is the sister group to the remainder of Cichlidae (Sparks and Smith, 2004).

In the study of Sparks and Smith (2004: fig. 1), four major cichlid subfamilial lineages were recovered, each of which received strong support. Etroplinae, endemic to Madagascar (*Paretroplus*) and southern Asia (*Etroplus*), was recovered as the sister taxon to the remainder of Cichlidae. The remaining Malagasy lineage, Ptychochrominae, is monophyletic and was recovered as the sister group to a clade comprising the African and Neotropical cichlids. The African (Pseudocrenilabrinae) and Neotropical (Cichlinae) lineages were each monophyletic and well supported in that reconstruction (Sparks and Smith, 2004).

In the current study, the "basal" members (i.e., sister taxa to the remaining members) of the African and Neotropical clades, *Heterochromis* and *Retroculus*, respectively, are included as outgroups, as well as members of all other Malagasy and South Asian cichlid genera. Morphological comparisons, however, were made to a broad range of cichlid and noncichlid taxa (a complete list of comparative material is presented in appendix 1). Monophyly of both the African and Neotropical cichlid lineages is well established, and it was not the goal of this study to resolve relationships within either of these

species-rich assemblages. The goal of this study was expressly to resolve relationships within the cichlid subfamily Etroplinae, and to provide morphological diagnoses for the subfamily and included subclades. In the discussions of character-state distributions, for the most part I restrict comment to the included taxa (appendix 1). Certain features present in Etroplinae, particularly those associated with a deep body (e.g., characters 11, 48, 49, 50, and 51), are also known to occur in other deep-bodied cichlid lineages (specifically the Neotropical genera *Pterophyllum* and *Symphysodon*). Given the family-level phylogenies that are available for Cichlidae (Farias et al., 1999, 2001; Sparks, 2001, 2004a; Sparks and Smith, 2004), all of which recover the African and Neotropical assemblages as monophyletic and well supported, the aforementioned morphological similarities are clearly homoplasious and not indicative of a close relationship between Etroplinae and certain deep-bodied Neotropical cichlid lineages. For example, if the deep-bodied Neotropical lineages had been included in the data matrix, these features would still optimize at the node for *Paretroplus*, except that they would be homoplasious instead of uniquely derived.

Morphological Characters: Coding

The morphological transformations reported in appendix 2 were coded from the examination of specimens listed in appendix 1. An attempt was made to code all morphological characters as binary, although this was not always possible and a few of the characters are multistate. All multistate characters were designated as unordered to avoid any a priori assumptions or models of character evolution. Missing (= unknown or unobservable) data in the matrix are designated by a "?". Characters were coded as missing or unknown if they could not be observed in the material available for examination. For example, if skeletal preparations or radiographs represented the only available study material, certain ligaments, cartilaginous structures, and external features were impossible to code, and were therefore designated as missing data in the matrix. Characters that could not be coded because they were inapplicable in a particular taxon (e.g., number of rows of teeth on the second pharyngobranchial tooth plates in taxa without second pharyngobranchial tooth plates, etc.), are designated by a "-" in the data matrix. The morphological data matrix was compiled with the use of MacClade vers. 3.0 (Maddison and Maddison, 1992) and 3.07 (Maddison and Maddison, 1997).

Text and Figure Abbreviations

The following abbreviations are used in the figures and text:

aa	anterior arm of first epibranchial
apps	adductor process of parasphenoid
a.s.l.	above sea level
av	anterior vertebrae
boc	basioccipital
cb4	fourth ceratobranchial
cb4-tp	fourth ceratobranchial tooth plate
cl	cleithrum
cpden	coronoid process of dentary
cor	coracoid
den	dentary
dfpt1	first dorsal-fin pterygiophore
eb1-4	epibranchials 1–4
eb2-tp	second epibranchial tooth plate
ect	ectopterygoid
ent	entopterygoid
exoc	exoccipital
exocf	exoccipital foramen
fm	foramen magnum
fr	frontal
gb	gas bladder
gbb	gas bladder bulla
gr	gill raker
hyo	hyomandibula
io2	second infraorbital bone
le	lateral ethmoid
max	maxilla
met	metapterygoid
mppvl	median palatoprevomerine ligament
nap	anterior neural arch processes
nlf_0	median frontal pores of neurocranium
pal	palatine
pb2-tp	second pharyngobranchial tooth plate

pb3-tp	third pharyngobranchial tooth plate
pc1-2	postcleithrum 1–2
pmax	premaxilla
pop	preopercle
pops	preopercular spine
ppang	primordial process of anguloarticular
ppml	proximal premaxillary-maxillary ligament
pro	prootic
ps	parasphenoid
qua	quadrate
sca	scapula
scl	supracleithrum
sep	supraoccipital-exoccipital prong
soc	supraoccipital
socn	supraoccipital notch
spml	second premaxillary-maxillary ligament
sn	supraneural
sym	symplectic
up	uncinate process of first epibranchial
up4-tp	fourth upper tooth plate
vm	vomer

Phylogenetic Analyses

For the phylogenetic analyses, nucleotide characters from the four gene fragments (16S, COI, Tmo-4C4, Histone H3) used by Sparks and Smith (2004) and 82 morphological transformations were simultaneously analyzed under the optimality criterion of parsimony with all transformations given equal weight. All nucleotide sequences were available on GenBank from prior studies by the author and colleagues (Farias et al., 1999, 2000; Sparks, 2004a; Sparks and Smith, 2004). Table 1 lists the GenBank numbers for all included nucleotide sequences. Because a tissue sample could not be obtained for *Paretroplus petiti* (known only from the formalin-fixed holotype), Sparks and Smith (2004) were unable to generate any sequence data for that taxon. Likewise, because a tissue sample could not be obtained for *Heterochromis multidens,* Sparks and Smith (2004) were unable to amplify the COI and histone H3 loci for this taxon. Therefore, *Heterochromis* is included here based on available GenBank sequences for 16S and Tmo-4C4. Missing gene fragments are designated as "unavailable" in table 1. Base positions corresponding to missing gene fragments are treated as missing data in the parsimony analyses.

A combined dataset comprising the nucleotide characters from the four genes used by Sparks and Smith (2004) and the 82 morphological transformations presented herein, but this time excluding *P. petiti*, was also analyzed using the same parameters as outlined below. Given that *Paretroplus petiti* is known only from the formalin-fixed holotype, this taxon lacks molecular sequence data, which could contribute to a lack of resolution (and decreased support) within the deep-bodied clade of *Paretroplus.* An analysis of the combined morphological and nucleotide dataset less *P. petiti* is presented simply to illustrate that relationships within the deep-bodied clade of *Paretroplus* are fully resolved and well supported in the absence of *P. petiti.*

These parsimony analyses were conducted using direct optimization (Wheeler, 1996) as implemented in the program POY (Wheeler et al., 2003), and run on the American Museum of Natural History Parallel Computing Cluster with default settings unless noted otherwise below. The method of direct optimization is used to avoid the potential biases inherent in standard sequence-alignment procedures (e.g., manual alignment), which may not necessarily result in the most-parsimonious topology due to a potentially suboptimal static input alignment (Slowinski, 1998; Wheeler, 2001). Unlike standard multiple sequence alignment, which is divorced from the search for optimal tree topologies, direct optimization combines alignment and tree-search into a single procedure (i.e., nucleotide homology is dynamic) to produce globally most-parsimonious trees.

The analysis began by generating 12 random addition sequences (RAS) per random replicate for 17 replicates. These 204 RAS were improved with TBR branch swapping during the searches, an additional round of TBR branch swapping of all trees within 0.5% of the shortest tree(s) found per replicate, and 340 parsimony ratchet replicates (Nixon, 1999; 20 rounds in each of the 17 replicates with ratchetpercent 20 and ratchetseverity 2 or 4). In addition to TBR

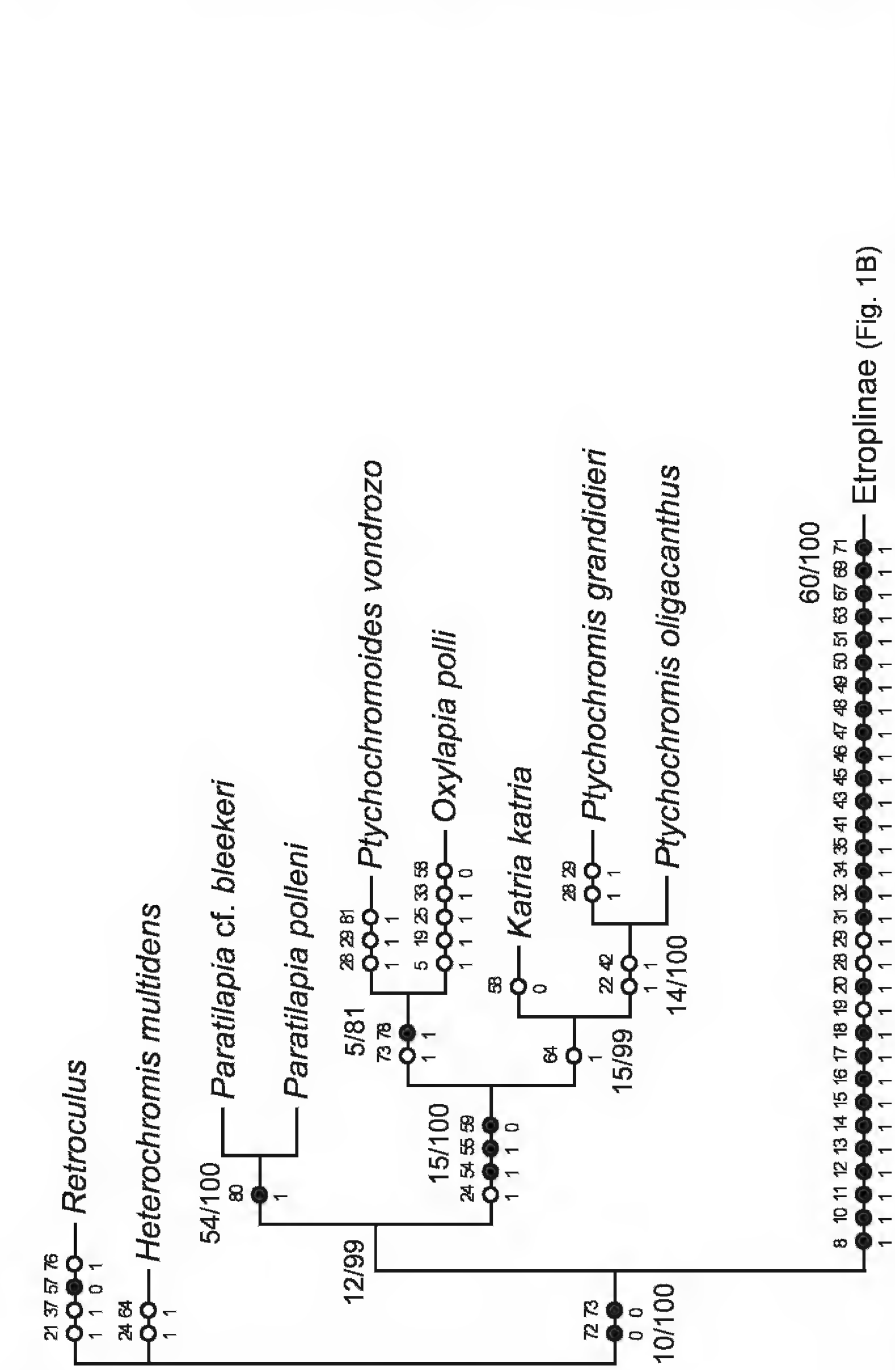
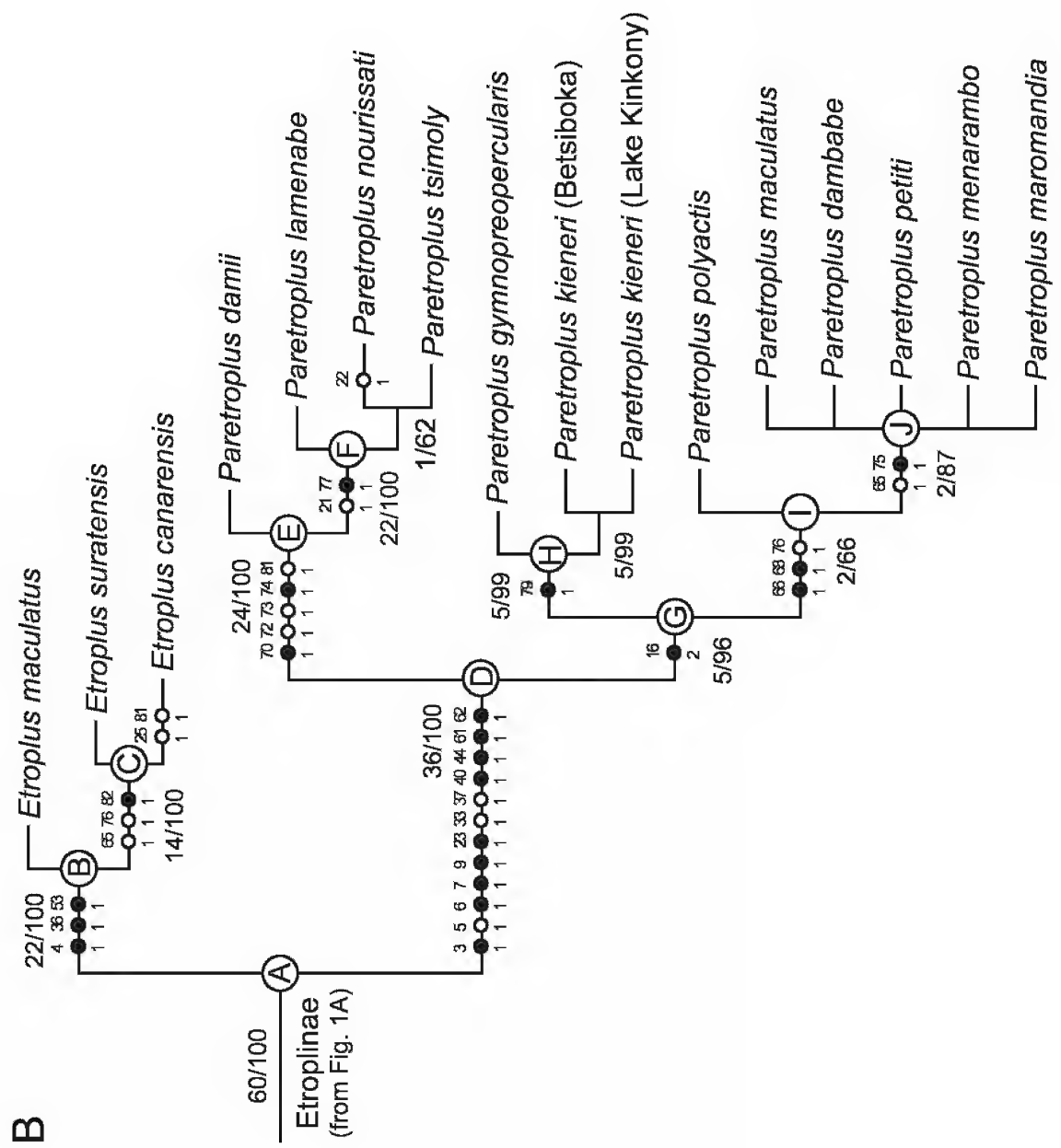


Fig. 1. Strict consensus cladogram depicting intrarelationships of Etroplinae based on the simultaneous analysis of 82 morphological transformations and 2025 aligned nucleotide characters from two mitochondrial (16S and COI) and two nuclear (histone H3 and Tmo-4C4) genes. The cladogram is split into two parts (A and B) to facilitate the visualization of morphological apomorphies. **A** (above), Apomorphic morphological features supporting monophyly of Etroplinae. **B** (below), Relationships within Etroplinae indicating apomorphic morphological features (phylogeny expanded from Fig. 1A). Character numbers for the morphological transformations correspond to those listed in the text (Results) and in appendix 2 (Morphological Character Matrix). See text for a discussion of the unambiguously optimized characters supporting each recovered node. Unique and unreversed synapomorphies are indicated by solid circles and homoplasious features by empty circles. Numbers next to branches indicate Bremer support (BS) and jackknife (JK) resampling percentages (> 50%) for each recovered node in the format of BS/JK.


B
Etroplus maculatus
Etroplus suratensis
Etroplus canarensis
Paretroplus damii
Paretroplus lamenabe
Paretroplus nourissati
Paretroplus tsimoly
Paretroplus gymnopreopercularis
Paretroplus kieneri (Betsiboka)
Paretroplus kieneri (Lake Kinkony)
Paretroplus polyactis
Paretroplus maculatus
Paretroplus dambabe
Paretroplus petiti
Paretroplus menarambo
Paretroplus maromandia
Etroplinae
(from Fig. 1A)
60/100
22/100
14/100
36/100
24/100
22/100
1/62
5/99
5/99
5/96
2/66
2/87
A
B
C
D
E
F
G
H
I
J

branch swapping and ratcheting within each replicate, all resulting trees within 1.0% of the shortest trees were examined in an additional round of TBR branch swapping. The random replicates from these initial searches resulted in five equally most-parsimonious trees. These five trees were submitted to POY for further tree searching using the commands iterative pass (Wheeler, 2003a) and exact (Wheeler et al., 2003), which reduce the heuristics in nucleotide optimization. This second step of the analysis began by tree fusing (Goloboff, 1999) the five submitted topologies and 20 additional RAS. The resulting trees were submitted to additional analyses including 100 rounds of parsimony ratcheting (ratchetpercent 20, ratchetseverity 2 or 5), and a final round of tree fusing and TBR branch swapping.

The length of the resulting implied alignment (Wheeler, 2003b) was verified in NONA (Goloboff, 1998) and PAUP* (Swofford, 2002). To estimate the "robustness" of the recovered phylogenetic hypotheses, Bremer supports (Bremer, 1988, 1995) were calculated using NONA and Tree Rot (Sorenson, 1999) in conjunction with PAUP*, and jackknife resampling analyses were performed using NONA (1000 replications, heuristic searches, 10 random additions per replication) via the WinClada interface (Nixon, 2000). Patterns of character evolution on the recovered topology were examined using NONA in conjunction with WinClada. Only unambiguous morphological transformations common to all most-parsimonious dichotomized trees are used to diagnose clades (Goloboff, 1995).

RESULTS

Phylogenetic Analyses

Simultaneous analysis of the 82 morphological transformations and 2025 nucleotide characters, based on the implied alignment (Wheeler, 2003b), resulted in five equally most-parsimonious trees with lengths of 1626 steps (498 parsimony-informative characters; consistency indices [CI, Kluge and Farris, 1969]: 0.55, and retention indices [RI, Farris, 1989]: 0.74 (when uninformative characters are retained). A strict consensus topology of these five optimal trees is presented in fig. 1. These five optimal trees differ only with respect to resolution within Clade J, which comprises most members of the deep-bodied lacustrine radiation of *Paretroplus* (i.e., among *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*). This lack of resolution is due to the fact that no molecular data could be collected for *P. petiti*, which is known only from the formalin-fixed holotype (see below). *Paretroplus petiti* is included here on the basis of morphological evidence only, which is insufficient for resolving relationships within this clade.

In this topology, Etroplinae (*Etroplus* + *Paretroplus;* Clade A) is monophyletic and extremely well supported. This transoceanic sister-group relationship between *Etroplus* (southern India/Sri Lanka) and *Paretroplus* (Madagascar) is supported by 31 unambiguously optimized morphological transformations, 28 of which are unique and unreversed, and has a Bremer support of 60 and a jackknife resampling percentage of 100%. Within Etroplinae, monophyly of *Etroplus* is strongly supported (Bremer support [BS] = 22; jackknife resampling percentage [JK] = 100%), as is monophyly of *Paretroplus* (BS = 36; JK = 100%), which is supported by 12 unambiguously optimized morphological transformations, nine of which are unique and unreversed. Within *Etroplus*, *E. suratensis* is recovered as the sister taxon to *E. canarensis*. These two species share three derived features that are absent in *E. maculatus* (see Discussion). Within *Paretroplus*, two major clades are recovered and receive strong support. Clade E comprises the generally shallow bodied rheophilic, riverine species *P. damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, new species (BS = 24; JK = 100%). Clade G comprises *P. kieneri* and *P. gymnopreopercularis*, which are relatively shallow-bodied and comparatively widespread in distribution, and the deep-bodied, disk-shaped and highly allopatric lacustrine species *P. polyactis*, *P. maculatus*, *P. dambabe*, *P. petiti*, *P. maromandia*, and *P. menarambo* (BS = 5; JK = 96). Interestingly, none of these six deep-bodied lacustrine species occur in sympatry.

For comparison, the combined dataset of 82 morphological features and 2025 nucleo-

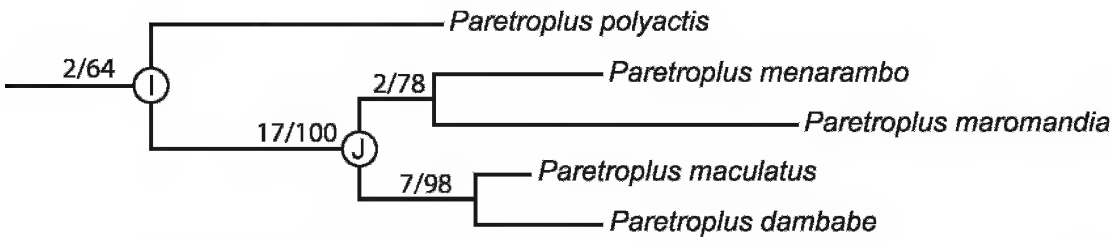


Fig. 2. Relationships within the deep-bodied clade (Clade J) in the absence of *Paretroplus petiti*, which lacks DNA sequence data. Simultaneous analysis of 82 morphological transformations and 2025 nucleotide characters resulted in a single, fully resolved hypothesis of relationships for Etroplinae (tree length of 1626 steps [499 parsimony-informative characters]; CI: 0.55 and RI: 0.74 [when uninformative characters are retained]) that is identical to that presented in Figure 1, except for within Clade J. Numbers next to branches indicate Bremer support (BS) and jackknife (JK) resampling percentages for each recovered node in the format of BS/JK.

tide characters was also analyzed using direct optimization (Wheeler, 1996) as implemented in the program POY (Wheeler et al., 2003) with the same search parameters as described above, but this time excluding *P. petiti*, which lacks molecular sequence data. Analysis of this combined dataset resulted in a single, fully resolved hypothesis of relationships for Etroplinae (tree length of 1626 steps [499 parsimony-informative characters]; CI: 0.55 and RI: 0.74 [when uninformative characters are retained]), and is presented to illustrate that relationships within the deep-bodied clade of *Paretroplus* are resolved in the absence of *P. petiti*, which was included in the combined analysis on the basis of morphological evidence only (fig. 2).

In this topology, relationships within the deep-bodied clade (Clade J) of *Paretroplus* are fully resolved. *Paretroplus dambabe* is recovered as the sister taxon to *P. maculatus*, whereas *P. maromandia* is the sister taxon to *P. menarambo* (fig. 2). All other relationships are identical to those recovered in the simultaneous analysis of morphological and nucleotide characters for all taxa (i.e., inclusive of *P. petiti*).

Following the individual character descriptions below, diagnoses are presented for each recovered clade (Discussion).

Characters

Morphological features are grouped into discrete anatomical units from anterior to posterior, according to general body region, and are numbered in sequence. The numbering of characters in the text corresponds to that presented in the character matrix (appendix 2). The assignment of a particular character state (e.g., zero, one, or two) to a taxon is not meant to imply that the feature is either plesiomorphic or derived in a global context, given that any such assignment is both dependent upon topology and taxon sampling. To be precise, these morphological transformations should be interpreted only within the context of the included terminals. It was neither feasible nor critical to the results of the present study to examine every species of cichlid. For each morphological transformation, character-state distributions are provided. For some features of interest, the presence of a particular character state is noted for taxa not included in the phylogenetic analyses. For each character, both the consistency index (CI) and retention index (RI) are provided in the format (CI, RI). When these indices are equivalent, only a single value is presented. The citations that follow many of the character headings indicate either the original source or relevant discussions for that feature. Character states discussed in the text are illustrated on the included figures. In all of the figures depicting anatomical structures cartilage is indicated by stippling.

Oral Jaws

1. *Outer premaxillary teeth.*

   0: Caniniform, small to moderate in size, generally uniform in diameter, tapering somewhat or abruptly at the tip (figs. 3A and 4A).

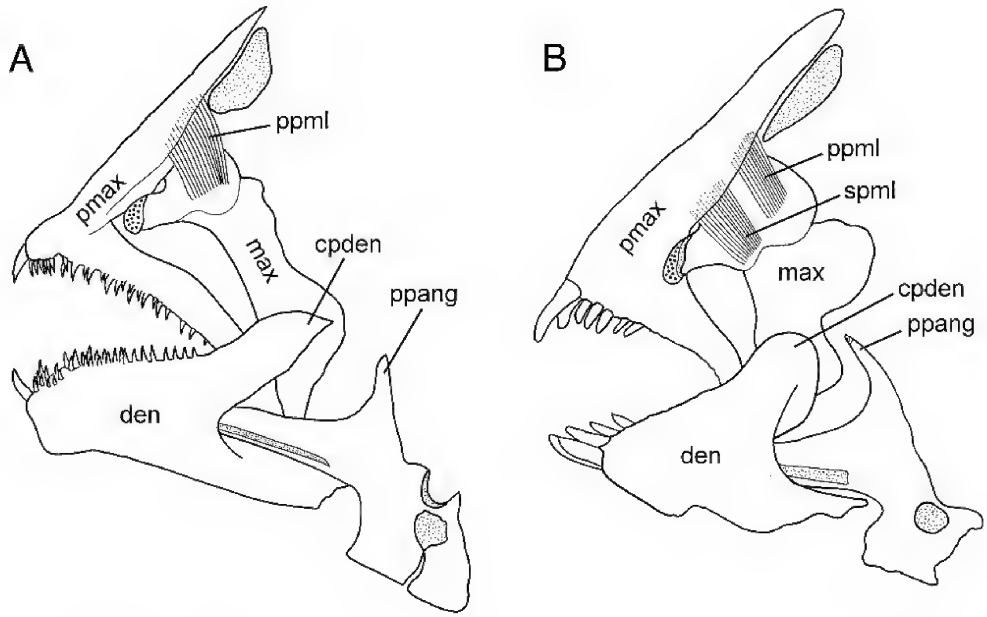


Fig. 3. Articulated right oral jaws in medial view: **A,** *Paratilapia* sp. "southeast", UMMZ 240359, C&S. **B,** *Paretroplus menarambo*, UMMZ 235014, C&S. Premaxillary-maxillary ligament(s) (ppml; spml) indicated by fine lines.

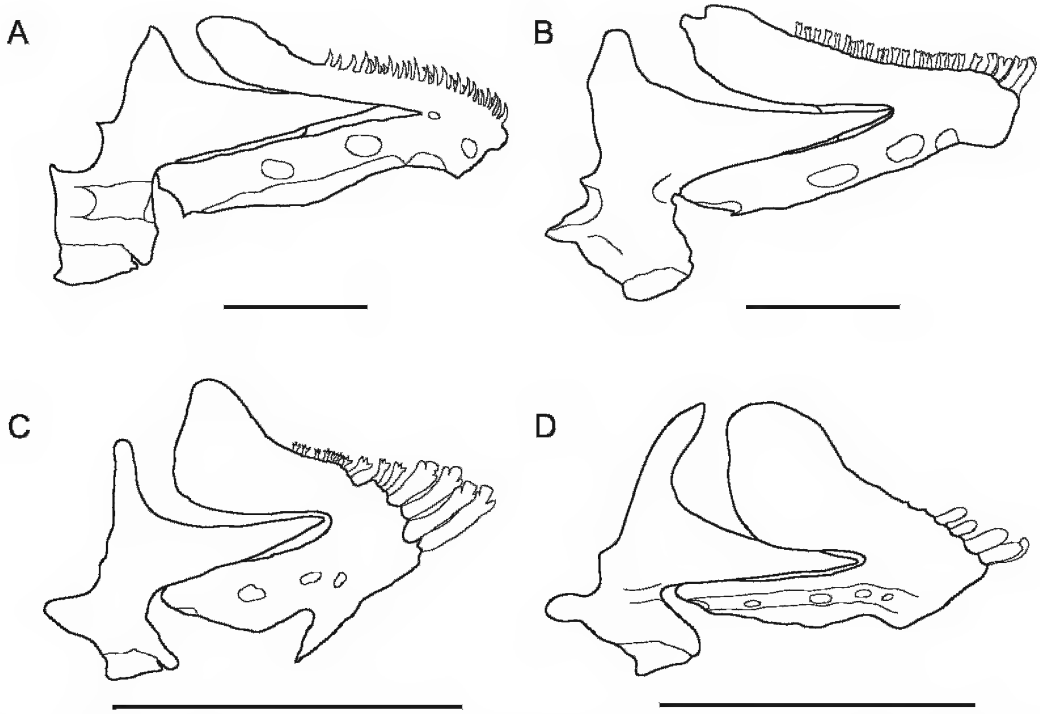


Fig. 4. Isolated right lower jaws in lateral view: **A,** *Heterochromis multidens*, MRAC 60893, C&S. **B,** *Ptychochromis grandidieri*, AMNH 88018, C&S. **C,** *Etroplus suratensis*, AMNH 217757, C&S. **D,** *Paretroplus gymnopreopercularis*, UMMZ 239532, C&S. Scale bars = 5 mm.

1: Outer premaxillary teeth anteroposteriorly flattened and broad at crown (figs. 3B and 4B–D).

Within Cichlidae, non-caniniform outer premaxillary teeth are restricted to the Malagasy–South Asian genera (less *Paratilapia*), a number of African lineages, and some Neotropical lineages. Within the Malagasy–South Asian genera oral teeth may be unicuspid (*Paretroplus* and *Paratilapia*) (figs. 3A and 4D), bicuspid (*Ptychochromis* and *Ptychochromoides*) (fig. 4B), or tricuspid (*Etroplus*) (fig. 4C). (0.50, 0.66)

2. *Oral jaw teeth bicuspid and bilaterally symmetrical, inner and outer rows of same morphology* (Cichocki, 1976; Reinthal and Stiassny, 1997; Sparks and Reinthal, 2001).

0: Absent.
1: Present.

Multiple rows of bilaterally symmetrical ("bifid") oral teeth, with inner and outer rows of the same morphology, are present only in ptychochromins (*Ptychochromoides* + *Oxylapia* + *Katria* + *Ptychochromis*, sensu Stiassny and Sparks, 2006) (fig. 4B), less *Oxylapia*. It is noteworthy that within a single individual, oral dentition in *Oxylapia* may range from wide flattened (particularly at the crown) unicuspid teeth, to bilaterally symmetrical bicuspid dentition as in *Ptychochromis* and *Ptychochromoides* (see Sparks and Reinthal, 2001: fig. 11b). *Oxylapia* possesses two inner rows of teeth in the upper jaw and a single inner row in the lower jaw. Inner row teeth in *Oxylapia* appear to all be unicuspid, elongate, and pointed, therefore, this taxon is herein coded as state zero for this feature. (0.50, 0.66)

3. *Single row of spatulate unicuspid oral dentition in both upper and lower jaws* (Cichocki, 1976; Reinthal and Stiassny, 1997; Sparks, 2001; Stiassny et al., 2001).

0: Absent.
1: Present.

State one is unique to *Paretroplus* (figs. 4D and 5A). In other cichlids exhibiting somewhat similar oral tooth morphology (e.g., *Chromidotilapia guentheri*, not included in phylogenetic analysis), these teeth are not only arranged in multiple rows, but they are much more numerous. (1.00)

Fig. 5. Articulated oral jaws in rostral view: **A,** *Paretroplus menarambo*, UMMZ 233522, S. **B,** *Paratilapia* sp., UMMZ 240366, S.

4. *Tricuspid oral dentition of same morphology in both inner and outer tooth rows* (Reinthal and Stiassny, 1997; Stiassny et al., 2001).

0: Absent.
1: Present.

Tricuspid teeth, in which both inner and outer rows on both upper and lower jaws are similar in morphology, are unique to *Etroplus* within Cichlidae (fig. 4C). All other cichlids examined lack similar oral dentition morphology. (1.00)

5. *Symphyseal premaxillary teeth elongate and enlarged.*

0: Absent.
1: Present.

In *Paretroplus*, markedly enlarged and elongate teeth are present on either side of the premaxillary symphysis (fig. 5A). Corresponding symphyseal teeth in the lower jaw are generally reduced in size to accommodate the enlarged premaxillary teeth. Within Cichlidae, enlarged symphyseal teeth are also present in *Oxylapia*. In the other genera examined, the symphyseal premaxillary teeth are not markedly enlarged relative to more lateral premaxillary teeth (fig. 5B). (0.50, 0.90)

6. *Distribution of oral dentition.*

0: Covering most of dentary and premaxillary arcade (figs. 3A and 4A–C).
1: Restricted anteriorly on premaxillary arcade and dentary (figs. 3B and 4D).

Oral dentition restricted to the rostral portions of both the premaxilla and dentary was observed only in *Paretroplus* and the South American genus *Chaetobranchopsis* (not included in phylogenetic analysis). (1.00)

7. *Number of teeth in upper and lower oral jaws.*

0: Teeth numerous (figs. 3A and 4A–C).
1: Very few teeth in both upper and lower jaws (figs. 3B and 4D).

Few oral teeth are present in all members of *Paretroplus* (18 or fewer in upper jaw, 14 or fewer in lower jaw), and in some deep-bodied Neotropical cichlids (i.e., *Chaetobranchopsis* and *Symphysodon*; not included in phylogenetic analysis). Oral jaw teeth are numerous in all other cichlid genera examined. (1.00)

8. *Dorsal process of anguloarticular.*

0: Not elongate (fig. 4A–B).
1: Dorsal process of anguloarticular (= primordial process in terminology of Barel et al., 1976) elongate (fig. 4C–D).

A markedly elongate anguloarticular process is restricted to Etroplinae (fig. 4C–D). This process is sickle-shaped and rostrally curved (i.e., concave along the anterior margin) in *Paretroplus*, and is also notably more elongate in *Paretroplus* than in *Etroplus*. (1.00)

9. *Apposition of dentary and dorsal process of anguloarticular.*

0: Coronoid process of dentary and dorsal (= primordial) process of anguloarticular widely separated (figs. 3A and 4A–C).
1: Posterior margin (= coronoid process) of dentary and dorsal (= primordial) process of anguloarticular closely apposed (figs. 3B and 4D).

Within Cichlidae, close approximation of the coronoid process of the dentary and the primordial process of the anguloarticular is restricted to *Paretroplus*. (1.00)

Ligaments Associated with the Oral Jaws

10. *Mesethmoid-maxillary ligament* (Cichocki, 1976).

0: Feeble and threadlike, or presumably absent.
1: Robust, straplike, and well developed.

Within Cichlidae a large, well-developed ligament passing from the rostral face of the mesethmoid and inserting on the maxilla, just dorsal of the anterior projection of the palatine prong (some fibers of this ligament may also attach to the rostral tip of the palatine prong) is restricted to Etroplinae and the Neotropical genus *Symphysodon* (not included in data matrix). In all other cichlids examined, this ligament is either weakly developed and threadlike, or presumably absent (i.e., it is often difficult to determine whether this ligament is either extremely feeble and threadlike or absent entirely). According to Cichocki (1976: character 11) this ligament is hypertrophied in the Neotropical genus *Symphysodon*, however, I find it more developed in *Paretroplus*. The mesethmoid-maxillary ligament is also notably elongate in *Paretroplus*. (1.00)

11. *Morphology of interopercular-mandibular ligament.*

0: The interopercular-mandibular ligament and the epihyal-interopercular ligament comprise two discrete ligaments with widely separated insertion points on the interopercle.
1: The interopercular-mandibular ligament is continuous with the epihyal-interopercular ligament (i.e., some fibers that originate as a continuous bundle on the retroarticular continue [unbroken] from the point of insertion of the

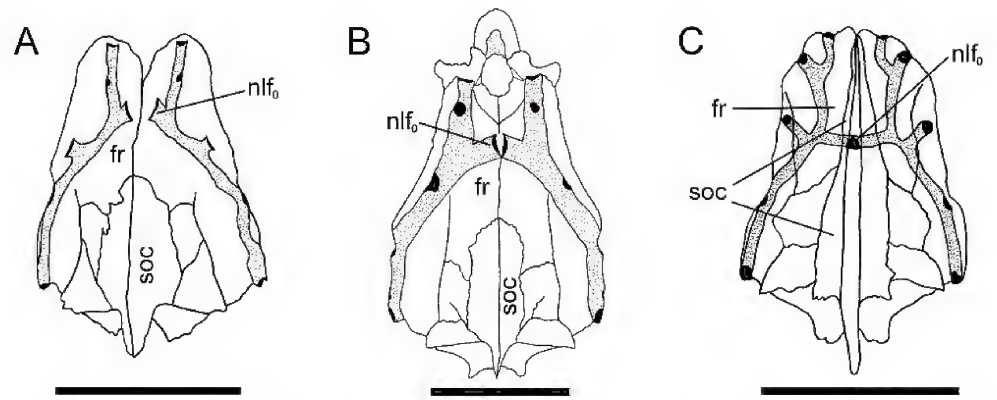


Fig. 6. Dorsal view of neurocranium illustrating configuration of neurocranial median frontal pores (nlf_0 of Barel et al., 1977): **A,** *Oxylapia polli*, UMMZ 235046, 78.0 mm SL. **B,** *Paratilapia polleni*, UMMZ 235043, 48.0 mm SL. **C,** *Paretroplus maculatus*, UMMZ 240364, 76.0 mm SL. Cephalic laterosensory canals indicated by stippling. Scale bars = 5 mm.

interopercular-mandibular ligament on the interopercle to insert on the epihyal).

In taxa exhibiting state one, there appear to be two discrete (or relatively discrete) and well-developed bundles of fibers originating on the caudal margin of the retroarticular: one bundle inserts on the anterior prong of the interopercle, whereas the other is weakly attached to the anterior prong of the interopercle, but continues essentially unbroken to insert on the epihyal, such that most fibers are not attached to the interopercle and pass continuously from the retroarticular to the epihyal. State one unites all members of Etroplinae, but is also reported in certain deep-bodied Neotropical cichlid genera, *Astronotus*, *Pterophyllum,* and *Symphysodon* (Sparks, 2001). The other Malagasy genera appear to fall out somewhere in between the condition observed in *Paretroplus* and the typical Neotropical and African configuration, in which the two ligaments are discrete and widely separated. (1.00)

12. *Number of "proximal" premaxillary-maxillary ligament(s).*

0: A single "proximal" premaxillary-maxillary ligament (fig. 3A).
1: The "proximal" premaxillary-maxillary ligament is composed of two distinct elements (fig. 3B).

In taxa exhibiting state one, in addition to the proximal premaxillary-maxillary ligament (terminology according to Anker, 1987), another broad and well-developed ligament passes from a more rostral origin on the maxilla (ca. the premaxillad wing) to insert into the groove of the premaxillary ascending process/spine (i.e., along the caudal and somewhat lateral margin of this bone) rostral to the proximal premaxillary-maxillary ligament (fig. 3B). In lateral view, this second ligament is located ventral and somewhat rostral to the proximal premaxillary-maxillary ligament. This second "proximal" premaxillary-maxillary ligament should not be confused with the distal premaxillary-maxillary ligament, which connects the maxilla (ventrally) to the posterior margin of the premaxilla. Other than members of Etroplinae no cichlids possess two discrete premaxillary-maxillary ligaments, although this feature is widely distributed in a number of noncichlid perciform outgroups examined. In the remaining Malagasy cichlid genera, the proximal premaxillary-maxillary ligament is robust, broad and sheetlike, but always a single element (fig. 3A). (1.00)

NEUROCRANIUM

13. *Median frontal canal(s) and pore(s) of neurocranium.*

0: Median frontal canals of neurocranium distinct, not forming a continuous tube; canals retain separate foramina (fig. 6A–B).

1: Median frontal canals coalesced and forming a continuous tube with a single dorsal foramen (= pore) (fig. 6C).

State one is restricted to Etroplinae, in which the median frontal canals are coalesced in the midline forming a continuous tube with a single dorsal foramen. Additionally, in these taxa, the single median frontal pore (nlf_0 pore(s) of Barel et al., 1977) is overlain completely by the supraoccipital bone (Stiassny, 1991), which extends quite far anteriorly (fig. 6C). In Etroplinae, the supraoccipital crest must be removed in order to reveal the underlying median frontal pore and portions of the median frontal canals, which are fused medially. In all other cichlid genera examined, and regardless of whether the median frontal pores meet in the midline (e.g., fig. 6B), the median canals of each frontal do not form a continuous tube and two distinct foramina (nlf_0 pore(s)) are retained. In these taxa the median frontal pores are not covered by the supraoccipital. (1.00)

14. *Greatly enlarged exoccipital foramina.*

0: Absent (fig. 7A–B).
1: Present (fig. 7C).

In Etroplinae (*Etroplus* + *Paretroplus*) the exoccipital foramina are greatly enlarged, and much of the exoccipital ossifications present in other cichlids are modified such that they form an internal, and dorsally projecting, exoccipital chamber (figs. 8A–B and 9B). The elaborate anterior gas bladder bullae characteristic of *Etroplus* and *Paretroplus* expand into and are lodged within these posterolaterally facing chambers. In all other cichlid taxa exhibiting any degree of enlargement of the exoccipital foramina, there is a simple opening to the interior of the skull, and an internal exoccipital chamber is lacking (fig. 8C and 9A). (1.00)

15. *Supraoccipital-exoccipital prong.*

0: Absent (fig. 10A).
1: Present (fig. 10B).

A ventrocaudally projecting supraoccipital-exoccipital prong, which extends ventrally over the foramen magnum, is present only in Etroplinae (figs. 7C and 10B), however, it is substantially less well developed in *Etroplus* than *Paretroplus*. This prong is composed primarily of supraoccipital ossifications, with some exoccipital contribution (to a variable degree), and is expanded distally. A similar structure is lacking in all other cichlid genera examined (figs. 7A–B and 10A). (1.00)

16. *Excavation of posterior margin of supraoccipital bone.*

0: Absent (fig. 10A).
1: Little excavation of bone, with incut either narrow and deep or exceedingly shallow.
2: Large wide and rounded excavation or incut on posterior margin of supraoccipital bone (= supraoccipital notch of Stiassny et al. [2001]) in lateral view (fig. 10B).

States one and two are restricted to members of Etroplinae. Members of both Etroplus and Clade E, *Paretroplus damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe* are coded as possessing state one (Stiassny et al., 2001: figs. 1d and 3a–b), although considerable intraspecific variation was observed within members of Clade E (i.e., the degree of supraoccipital excavation in some lacustrine populations of *P. damii* approaches state two, whereas riverine species, e.g., *P. nourissati*, are generally characterized by a nearly imperceptible degree of excavation). All remaining species of *Paretroplus* (i.e., members of Clade G) exhibit state two (fig. 10B). (1.00)

17. *Foramen magnum.*

0: Not enlarged (figs. 7A–B and 9A).
1: Foramen magnum (= occipital foramen) greatly enlarged (figs. 7C and 9B).

State one is restricted to Etroplinae. In members of this clade not only is the foramen magnum greatly enlarged, but the roof (= vault, following terminology of Stiassny et al., 2001) of the structure is significantly reduced (figs. 7C and 9B). (1.00)

18. *Frontal bones overlain by supraoccipital bone.*

0: Frontal bones not covered by supraoccipital medially (fig. 6A–B).
1: Frontal bones overlain and bisected by supraoccipital bone along their medial margin (except at rostral margin of frontals) (fig. 6C).

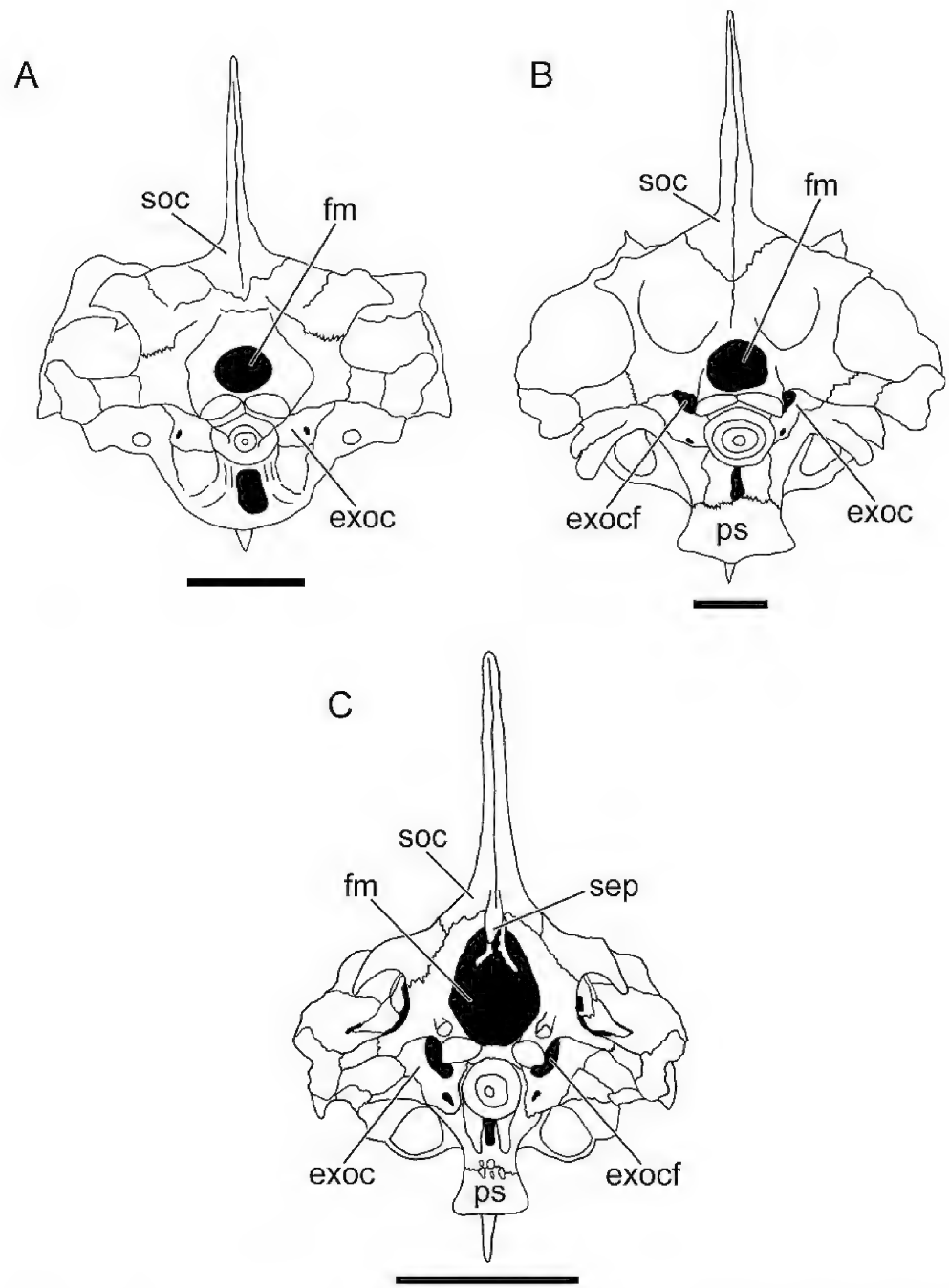


Fig. 7. Posterior view of neurocranium: **A,** *Heterochromis multidens*, MRAC 60893, C&S. **B,** *Ptychochromoides betsileanus*, UMMZ 238115, S. **C,** *Paretroplus damii*, UMMZ 233523, S. Scale bars = 5 mm (A and B), and 10 mm (C).

State one is restricted to Etroplinae in which the supraoccipital extends nearly to the anterior margin of the frontals. In all other cichlid genera examined the supraoccipital is restricted posteriorly and a majority of the median margin of the frontal bones is not covered by the supraoccipital. (1.00)

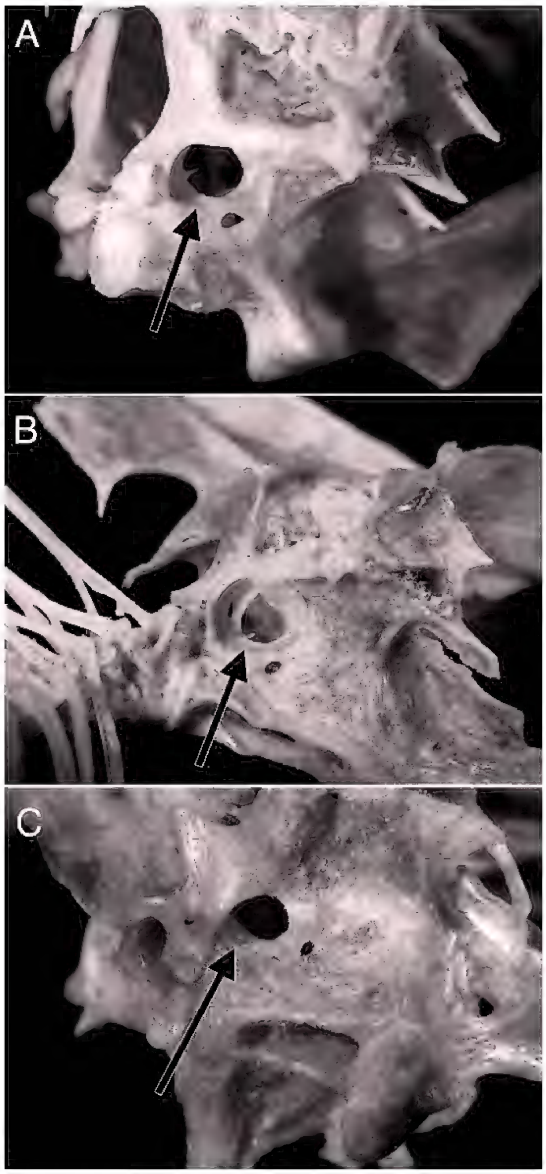


Fig. 8. Ventrolateral view of neurocranium illustrating exoccipital recesses in: **A,** *Paretroplus damii*, UMMZ 233523, S. **B,** *Paretroplus menarambo*, UMMZ 233522, S. **C,** *Ptychochromoides betsileanus*, UMMZ 238115, S. Arrows point to exoccipital foramina. Note complex exoccipital excavation in *Paretroplus* composed of both an inner and outer chamber.

19. *Ethmovomerine morphology.*

0: Shallow bodied and elongate (fig. 10A).
1: Deep bodied and truncate (fig. 10B).

In taxa exhibiting state one, the ethmovomerine assemblage is robust, deep bodied, and truncate, lending a beaked (i.e., convex and rounded) appearance to the structure in lateral view. State one is quite pronounced in *Paretroplus*, less so in *Etroplus*, and is also present in *Oxylapia* and the African taxon *Tropheus moorei* (not included in phylogenetic analysis). (0.50, 0.85)

20. *Ventral laminar extension of median keel (= adductor process) of parasphenoid.*

0: Absent (fig. 10A).
1: Present (fig. 10B).

Within cichlids, an expansive, ventrally projecting (keel-like) laminar adductor process, resembling an inverted triangle in lateral view, is present in all members of Etroplinae and also in the Neotropical genus *Symphysodon* (fig. 10B). The adductor process of the parasphenoid serves as an attachment point for the adductor arcus palatini (Rosen and Patterson, 1990, review the distribution of a parasphenoid adductor process). In all other genera examined the adductor process is shallow bodied (fig. 10A). (1.00)

21. *Elongate nasal bones.*

0: Absent.
1: Present.

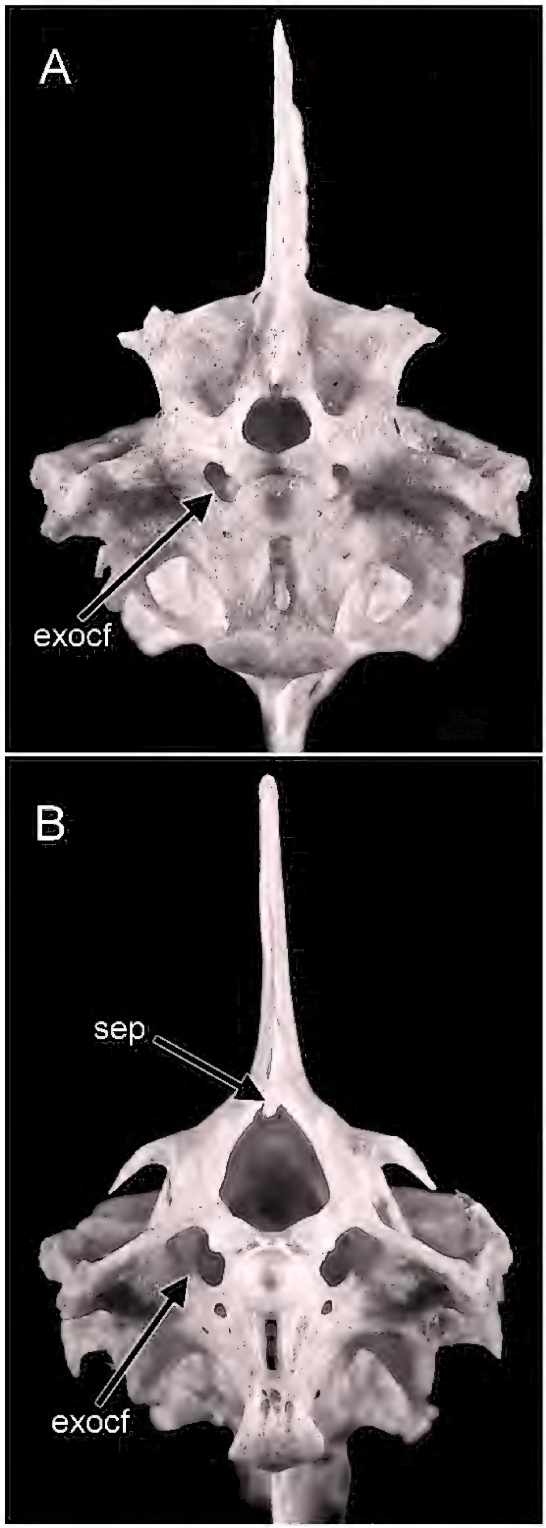
Markedly elongate nasal bones are present only in members of Clade F, comprising *Paretroplus nourissati*, *P. tsimoly*, and *P. lamenabe*, as well as in the Neotropical genus *Retroculus* and in some Neotropical geophagines. (0.50, 0.66)

Gill Arches

22. *Uncinate process of first epibranchial bone shorter than anterior arm* (Cichocki, 1976; Stiassny, 1991).

0: Absent.
1: Present.

Within Cichlidae, a shorter uncinate process is present only in the Malagasy genus *Ptychochromis* (e.g., fig. 11B) and in *Paretroplus nourissati*. In all other Malagasy–South Asian cichlids, the two arms are about equal



in length (fig. 11C–D). An uncinate process that is longer than the anterior arm is present in all African cichlids, less *Heterochromis* in which the two arms are equal in length, and also in several Neotropical genera. (0.50)

23. *Articulation of pharyngobranchial one and neurocranium.*

0: First pharyngobranchial articulates with prootic only.
1: First pharyngobranchial articulates with parasphenoid only or at parasphenoid-prootic margin.

Articulation of the first pharyngobranchial to either the parasphenoid or the parasphenoid-prootic margin is unique to *Paretroplus*. The first pharyngobranchial articulates with the prootic only (i.e., there is no parasphenoid contact) in all other cichlids, less the Neotropical genus *Crenicichla* (not included in phylogenetic analysis) in which there is no articulation of the first pharyngobranchial and the neurocranium. (1.00)

24. *Rostral extension of second basibranchial bone.*

0: Second basibranchial extends rostral of first hypobranchial bones.
1: Second basibranchial does not extend anterior of first hypobranchial bones (in dorsal view).

State one is present in the ptychochromine genera *Ptychochromis*, *Ptychochromoides*, and *Oxylapia*, however, the condition is not unique to these lineages within Cichlidae (also occurring in a few African and Neotropical genera). (0.50, 0.80)

25. *Fourth ceratobranchial tooth plates.*

0: Absent.
1: Median tooth plates not well developed and cover less than half of ossified portion of fourth ceratobranchial bones (i.e., restricted centrally on ceratobranchial four) (fig. 12A).
2: Tooth plates well developed and cover well over half to nearly entire dorsal

←

Fig. 9. Posterior view of neurocranium: **A,** *Ptychochromoides betsileanus*, UMMZ 238115, S. **B,** *Paretroplus damii*, UMMZ 233523, S.

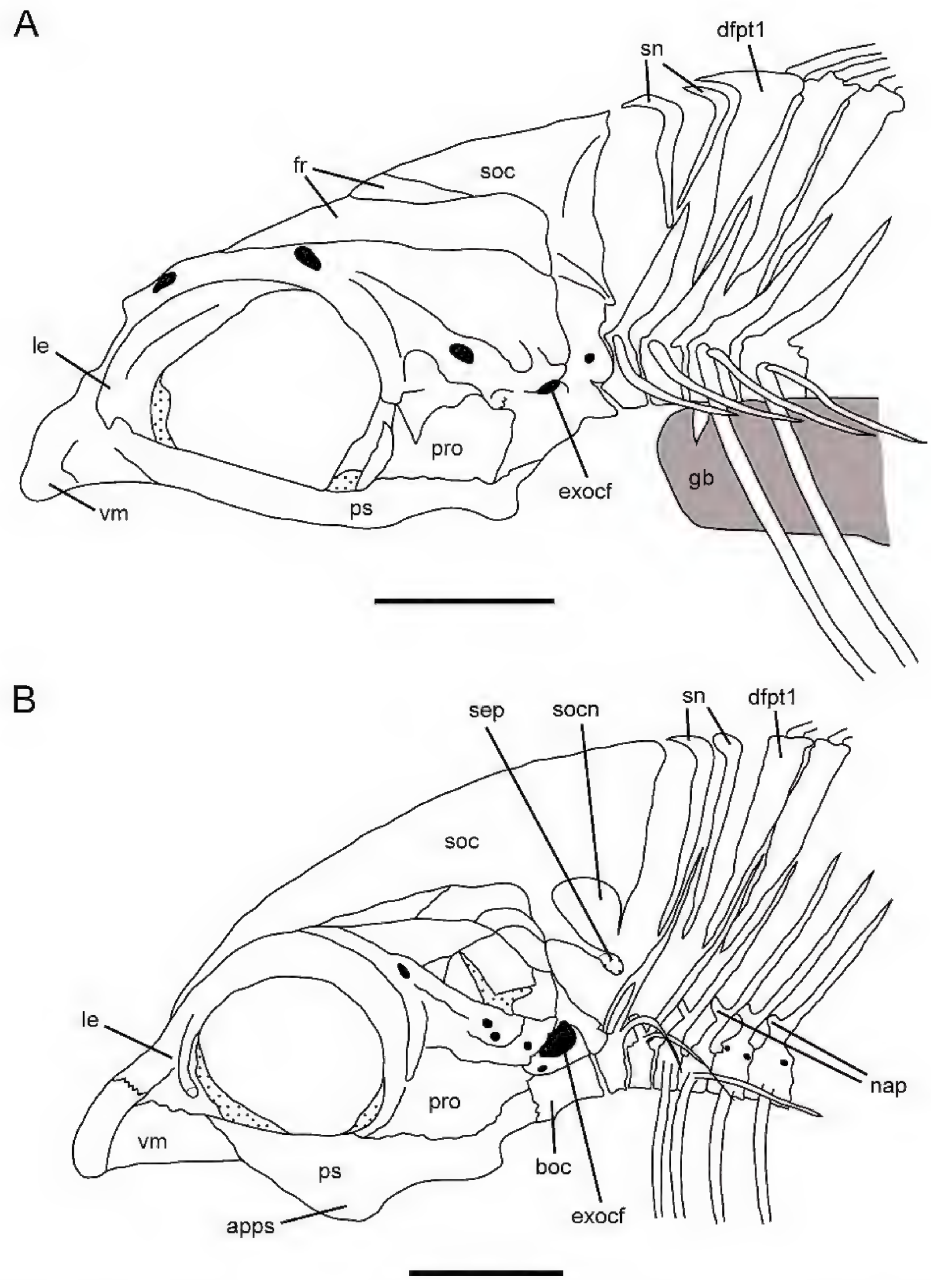


Fig. 10. Lateral view of neurocranium: **A,** *Katria katria*, UMMZ 240358, C&S. **B,** *Paretroplus dambabe*, UMMZ 235024, C&S. Scale bars = 5 mm. Rostral extent of paired anterior gas bladder chambers in *Katria katria* (only left chamber illustrated) indicated by shading.

surface of fourth ceratobranchial bones (fig. 12B).

State two is present in all Malagasy–South Asian taxa with the exception of *Paratilapia* (which lacks fourth ceratobranchial tooth plates), *Etroplus canarensis* (state 1), and *Oxylapia* (state 1). State one is widespread in Neotropical cichlids, whereas an absence of fourth ceratobranchial tooth plates is common to all African cichlids. (0.40, 0.25)

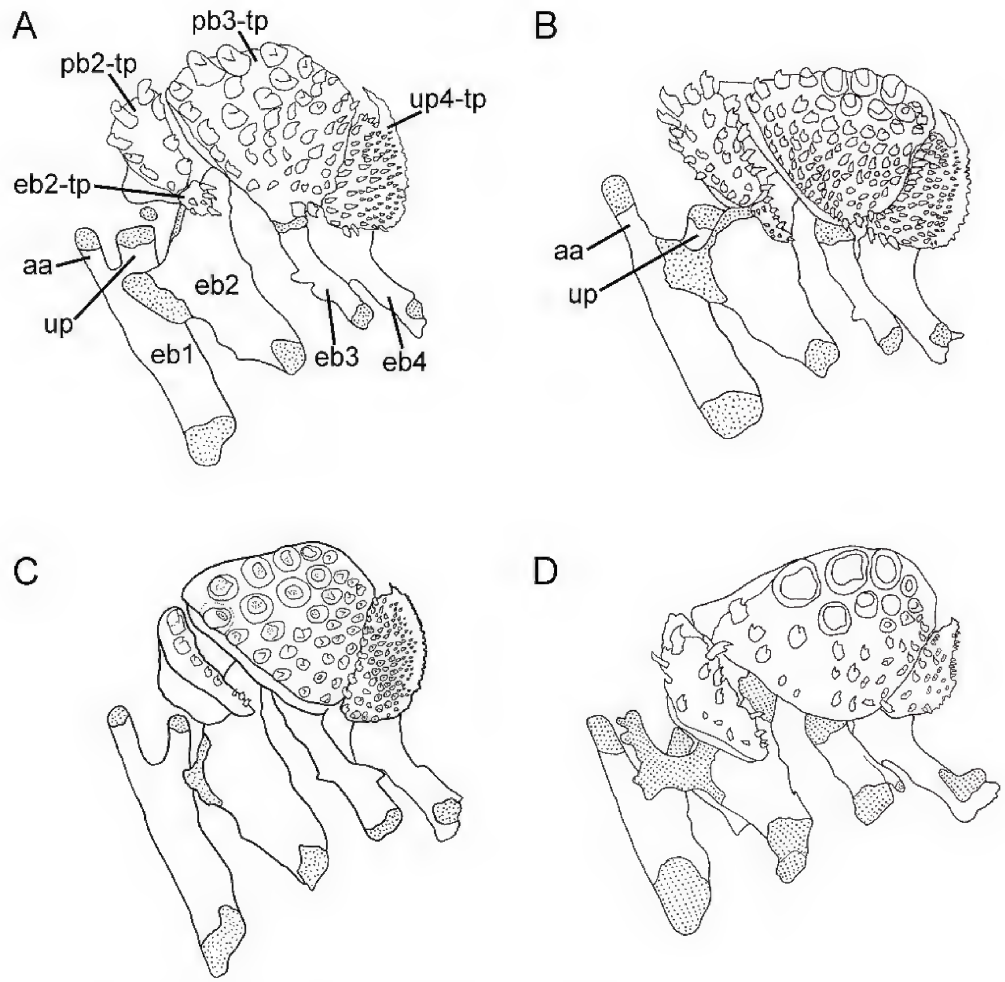


Fig. 11. Isolated right upper pharyngeal elements in ventral view: **A,** *Ptychochromis inornatus*, UMMZ 237064, C&S. **B,** *Ptychochromis grandidieri*, UMMZ 237312, C&S. **C,** *Ptychochromoides vondrozo*, UMMZ 235294, C&S. **D,** *Paretroplus dambabe*, UMMZ 235024, C&S.

26. *Fourth ceratobranchial tooth plates separate from outer row of gill rakers.*

0: Tooth plates confluent with outer row gill rakers (fig. 12B).
1: Tooth plates separate from outer row gill rakers (fig. 12A,C).

State one is unique to Etroplinae, the monotypic Malagasy genus *Oxylapia*, as well as the Neotropical genus *Retroculus*. Although the fourth ceratobranchial tooth plates in Etroplinae and *Oxylapia* are heavily ossified and expansive, with numerous teeth per plate, they are not confluent with the outer row (= lateral) gill rakers of the fourth ceratobranchial bones (fig. 12C). (0.50, 0.66)

27. *Hooked and bicuspid fourth ceratobranchial teeth.*

0: Absent.
1: Present.

Hooked and bicuspid fourth ceratobranchial teeth are present in all Malagasy–South Asian cichlids (figs. 12B–C and 13), with the exception of *Paratilapia*, which lacks fourth ceratobranchial tooth plates. In species exhibiting state one, the fourth ceratobranchial teeth become more strongly hooked and bicuspid medially on the tooth plates, where-

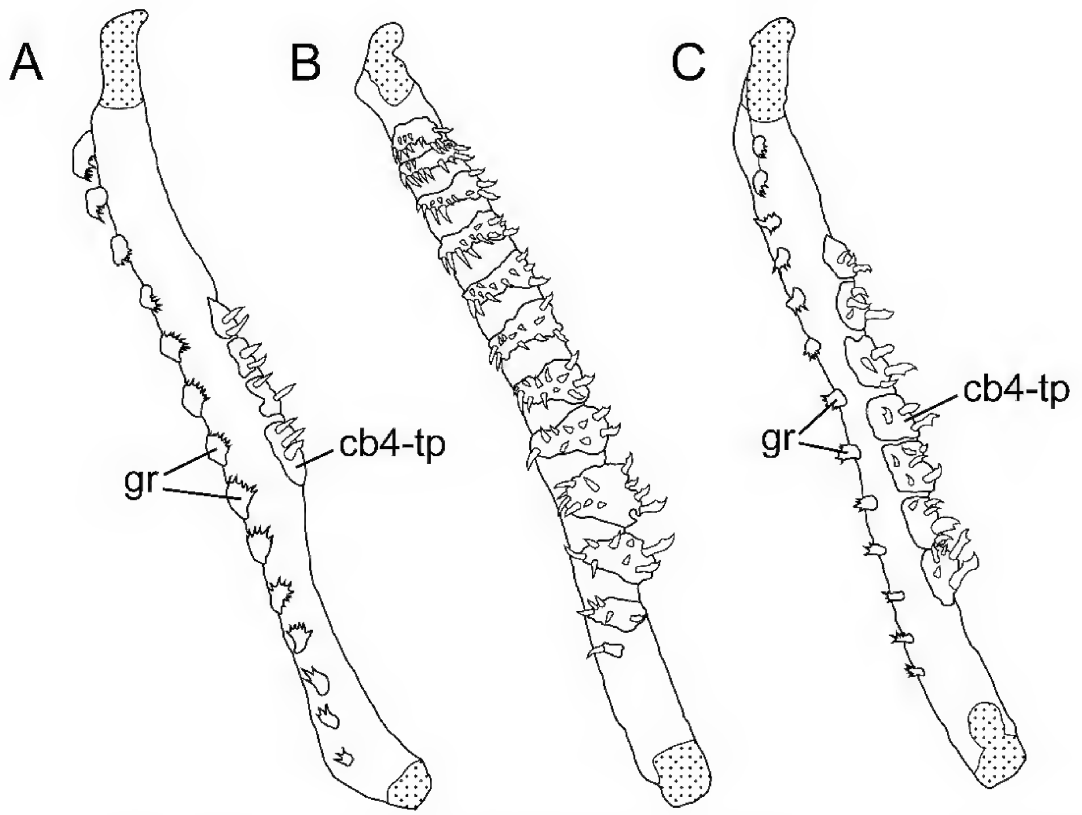


Fig. 12. Isolated right fourth ceratobranchial elements in dorsomedial view: **A,** *Retroculus lapidifer*, MNRJ 12910, C&S. **B,** *Ptychochromis inornatus*, UMMZ 237064, C&S. **C,** *Paretroplus nourissati*, UMMZ 235206, C&S.

as these teeth are frequently conical laterally (fig. 12B). Although Kullander (1998: 473–474) reported that no cichlid species other than *Ptychochromis oligacanthus* possesses anything but conical teeth on these tooth plates, in fact, in addition to all Malagasy–South Asian cichlids (less *Paratilapia*), hooked and bicuspid fourth ceratobranchial teeth are also present in the Neotropical cichlids *Geophagus surinamensis* and *Pterophyllum*. All other genera examined with fourth ceratobranchial tooth plates possess only conical teeth (fig. 12A). (Uninformative in current analysis)

28. *Molariform teeth on third pharyngobranchial tooth plates.*

0: Absent.
1: Present.

Although not unique to Etroplinae within Cichlidae, the third pharyngobranchial tooth plates bear molariform teeth (or nearly molariform teeth in *Paretroplus nourissati*, *P. tsimoly*, and *Etroplus canarensis*) in all members of this clade (fig. 11D). Molariform teeth on the third pharyngobranchial tooth plates were also observed in some members of the Malagasy genera *Ptychochromis* and *Ptychochromoides* (e.g., fig. 11C), but not in all species of these genera (e.g., fig. 11A–B). Apart from the Malagasy–South Asian cichlids, state one was observed only in the African genus *Tylochromis* (not included in phylogenetic analysis). (0.33, 0.66)

29. *Molariform teeth on fifth ceratobranchial tooth plates.*

0: Absent.
1: Present.

Although not unique to Etroplinae within Cichlidae, molariform teeth are present on the fifth ceratobranchial tooth plates in all

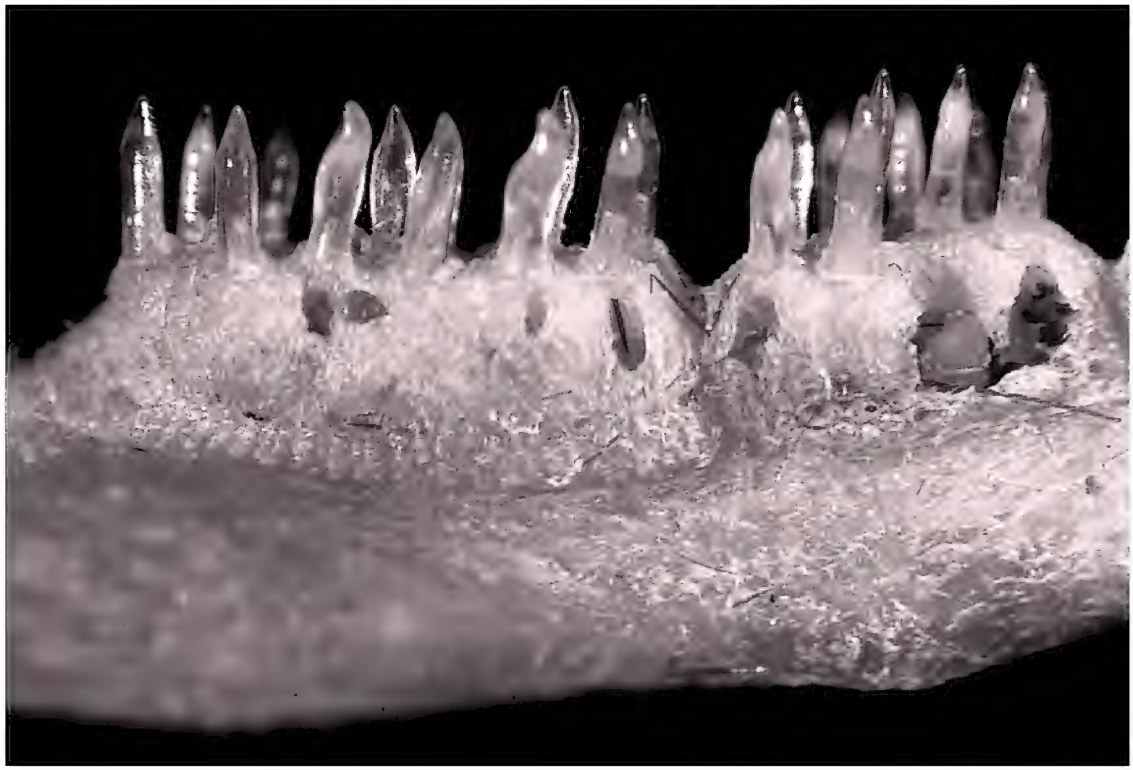


Fig. 13. Photograph of dentition on fourth ceratobranchial tooth plates in lateral view in *Paretroplus damii*, UMMZ 233523, S.

members of this clade [or nearly molariform in *Etroplus canarensis*, for which all C&S specimens available are relatively small (< 75 mm SL)] (fig. 14B). Molariform teeth on the fifth ceratobranchial tooth plates are also present in some members of the Malagasy genera *Ptychochromis* and *Ptychochromoides* (e.g., fig. 14A). (0.33, 0.66)

30. *Strong concavity on medial margin of fourth upper tooth plate forming well-developed, medially directed prong.*

    0: Absent.
    1: Present.

A pronounced, rounded concavity and medially directed, sickle-shaped prong or spine is present on the caudomedial margin of the fourth upper tooth plate in all Malagasy cichlids (fig. 11), and also in the Neotropical cichlid *Geophagus surinamensis* (not included in phylogenetic analysis). This concavity is absent in the South Asian genus *Etroplus*. (0.50, 0.75)

31. *Central ligament of ventral branchial apparatus bifurcate over entire length.*

    0: Absent.
    1: Present.

Within Cichlidae state one is unique to Etroplinae. In Etroplinae the central ligament is bifurcate over its entire length (i.e., separate from its origin on the anterior tips of the fifth ceratobranchial elements), and in effect comprises two distinct ligaments. In taxa exhibiting state zero, the central ligament is either a single band, or it may split anteriorly near its rostral insertion point (i.e., a single ligament becomes bifurcated only anteriorly). (1.00)

32. *Urohyal morphology.*

    0: Urohyal tripartite, ventral flanges oriented ventrolaterally, or enlarged and mostly horizontal.
    1: Ventral flanges greatly reduced in width laterally (i.e., flanges very narrow) and oriented horizontally, such that the urohyal is flat ventrally.

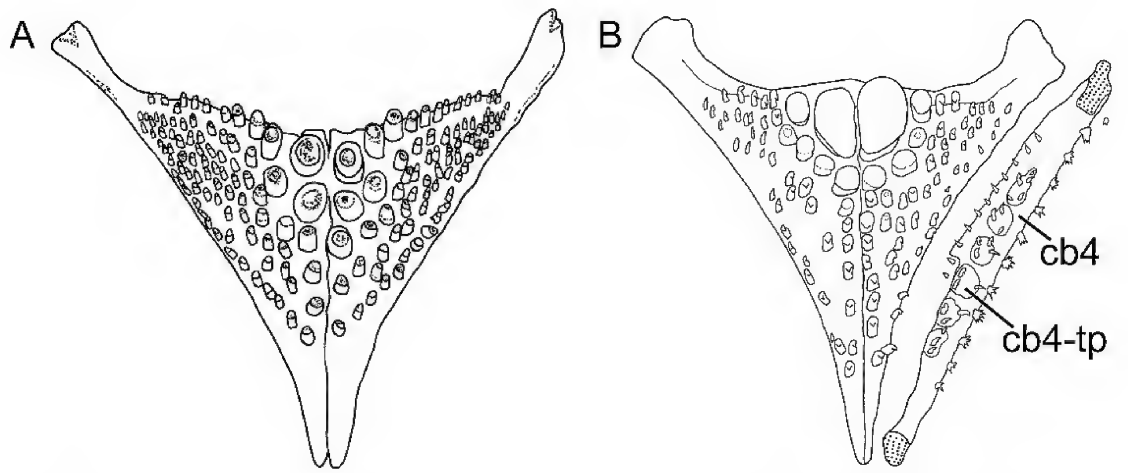


Fig. 14. Lower pharyngeal jaws (= fused fifth ceratobranchial elements) in dorsal view: **A,** *Ptychochromoides vondrozo*, UMMZ 235294, C&S. **B,** *Paretroplus dambabe*, UMMZ 235024, C&S (also illustrating left fourth ceratobranchial).

Within Cichlidae, state one is restricted to Etroplinae in which the ventral flanges are quite narrow. (1.00)

SUSPENSORIUM (*INCLUDING INFRAORBITAL SERIES AND LIGAMENTS CONNECTING THE PALATINE TO THE NEUROCRANIUM AND LACRIMAL*)

33. *Maxillary process of palatine* (Cichocki, 1976).

0: Not reduced in diameter rostrally (fig. 15A).
1: Elongate, slender over entire length, and tapered rostrally (fig. 15B).

State one is restricted to the Malagasy genera *Paretroplus* and *Oxylapia*. Many cichlids possess an elongate and thin maxillary palatine process, but unlike the condition in *Paretroplus* in which the maxillary process becomes markedly tapered rostrally, the maxillary process is never tapered in these other cichlid genera. (0.50, 0.90)

34. *Lateral insertion of median palatovomerine ligament* (Cichocki, 1976; Kullander, 1996; Sparks, 2001).

0: Entirely on palatine.
1: Primarily on entopterygoid, and only weakly on ectopterygoid.

A median palatovomerine (= palatoprevomerine) ligament inserting primarily on the entopterygoid, and only weakly on the ectopterygoid, is restricted to Etroplinae (fig. 15B). In the Neotropical genus *Crenicichla* (not included in phylogenetic analysis), the median palatovomerine ligament inserts strongly on the ectopterygoid and very weakly on the palatine, whereas in the Neotropical genus *Teleocichla* (also not included in phylogenetic analysis), the median palatovomerine ligament inserts entirely on the ectopterygoid and the palatine is displaced dorsally (Kullander, 1988). (1.00)

35. *Apposition of palatine and vomerine head.*

0: Palatine closely apposed to posterolateral margin of prevomerine head.
1: Palatine displaced dorsally, ectopterygoid and entopterygoid relatively more closely associated with posterior margin of prevomerine head than palatine.

In taxa exhibiting state one, the median palatovomerine ligament bypasses the palatine to insert on the entopterygoid and ectopterygoid. Within Cichlidae, state one is restricted to Etroplinae and the Neotropical genus *Crenicichla* (not included in phylogenetic analysis). (1.00)

36. *Number of lacrimal plates* (Cichocki, 1976; Stiassny, 1991: figs. 1.13 and 1.14).

0: Two, comprising lacrimal proper and plate-like "primitive second infraorbital" of Cichocki (1976).

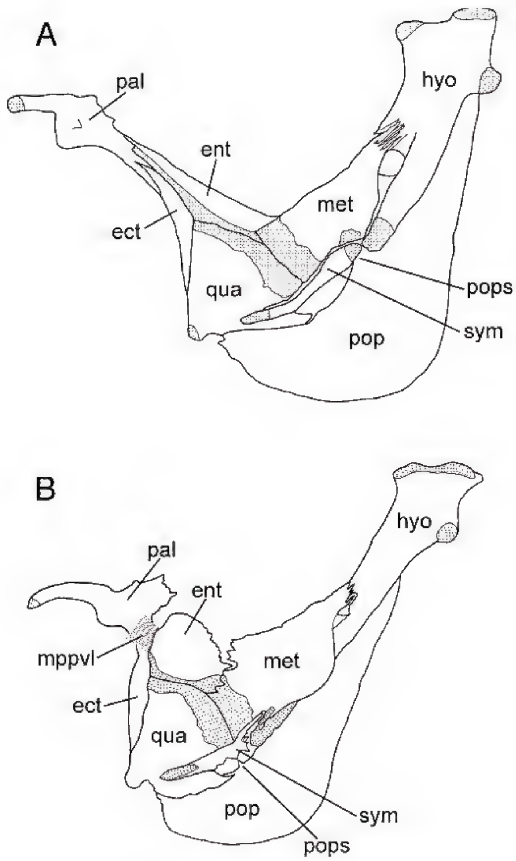


Fig. 15. Isolated right suspensorium in medial view. **A,** *Paratilapia polleni*, UMMZ 235043, C&S. **B,** *Paretroplus menarambo*, UMMZ 235014, C&S. Median palatovomerine ligament indicated by closely set parallel lines.

1: One, comprising lacrimal proper.

In general, cichlids possess a single lacrimal, the next infraorbital bone (= second infraorbital, io2) being shallow and tubular, and followed posteriorly by the third to fifth infraorbitals and the dermosphenotic (fig. 16E). In taxa exhibiting state zero, the first two infraorbital bones in series, comprising the lacrimal and io2, are broad and platelike (fig. 16A–D). Two "lacrimal" plates (i.e., lacrimal proper and io2) are found in all Malagasy cichlids (e.g., fig. 16C–D), the Neotropical genera *Retroculus* (fig. 16A), *Cichla*, and *Astronotus* (see below), as well as the monotypic African genus *Heterochromis* (fig. 16B). In these taxa, the "lacrimal" is essentially comprised of two broadly contiguous plates (i.e., a second expansive and more or less platelike, canal-bearing bone is situated posterior to and abuts the lacrimal proper). In taxa with two lacrimal plates, the third infraorbital bone in series (= second infraorbital of Stiassny, 1991: 22) is shallow and tubular, and generally followed by three additional infraorbitals and the dermosphenotic. In *Astronotus*, the degree of fusion (= co-ossification) between the two lacrimal plates is highly variable, and these bones may appear as a single element in some specimens (e.g., see Kullander, 1998: 478). The South Asian genus *Etroplus* and all other African and Neotropical cichlids have a single lacrimal plate (fig. 16E). (1.00)

37. *Lacrimal shape.*

0: Essentially square or rectangular, and not anteroventrally expanded (fig. 16B–C, E).
1: Anteroventrally expanded, elongate, and resembling a paddle (fig. 16A, D).

An elongate, paddle-shaped lacrimal (i.e., anterior lacrimal plate; see Character 36 above) is found only in the Malagasy genus *Paretroplus* (fig. 16D) and the Neotropical genus *Retroculus* (fig. 16A). (0.50, 0.90)

38. *Lacrimal lateral line canals.*

0: Canals short, foramina not constricted (fig. 16A–C).
1: Lateral line canals elongate, foramina of canals narrow or constricted (fig. 16D–E).

Within Cichlidae, state one is restricted to members of Etroplinae (less *Etroplus maculatus*), and is more pronounced in *Paretroplus* (fig. 16D) than *Etroplus* (fig. 16E). (0.50, 0.88)

39. *Marginal canal between lacrimal plates* (Stiassny, 1991).

0: Well developed (fig. 16A–C).
1: Markedly reduced or absent (fig. 16D).

State one is unique to *Paretroplus*. Regardless of the number of lacrimal plates (*Paretroplus* possesses two [Character 36]), *Paretroplus* is the only taxon to possess a second infraorbital (i.e., here the second lacrimal plate) that is oriented along the long axis of the lacrimal (i.e., extending antero-

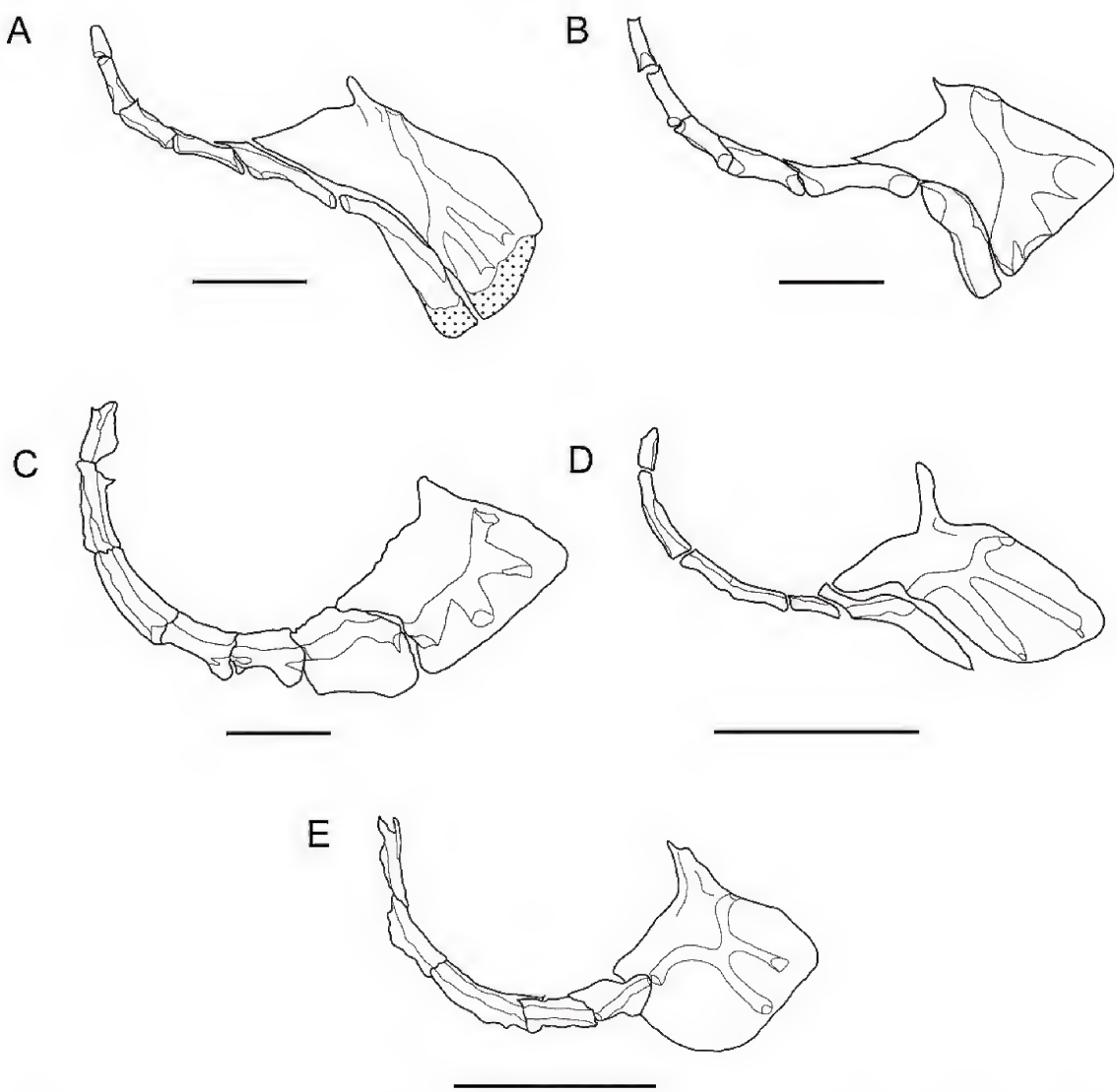


Fig. 16. Isolated right infraorbital series in lateral view. **A,** *Retroculus lapidifer*, MNRJ 12910, C&S. **B,** *Heterochromis multidens*, MRAC 60893, C&S. **C,** *Ptychochromoides vondrozo*, UMMZ 235294, C&S. **D,** *Paretroplus nourissati*, UMMZ 235206, C&S. **E,** *Etroplus canarensis*, AMNH 233642, C&S. Scale bars = 5 mm.

ventrally), and in which the marginal canal between these bones is either poorly developed or absent (fig. 16D). Although *Retroculus* and *Heterochromis* also have two lacrimal plates and a similarly oriented second infraorbital bone (i.e., second lacrimal plate), in these taxa the marginal canal between the lacrimal plates is well developed (fig. 16A–B). (1.00)

40. *Entopterygoid flange.*

0: Absent.
1: Present.

In taxa exhibiting state one, the entopterygoid bears a flange or "calyx" on the anterodorsal portion of the bone, which partially overlies the dorsomedial surface of the ectopterygoid, forming a slot into which the median palatoprevomerine (= palatovomerine) ligament inserts (fig. 15B). Within Cichlidae, state one is unique to *Paretroplus*.

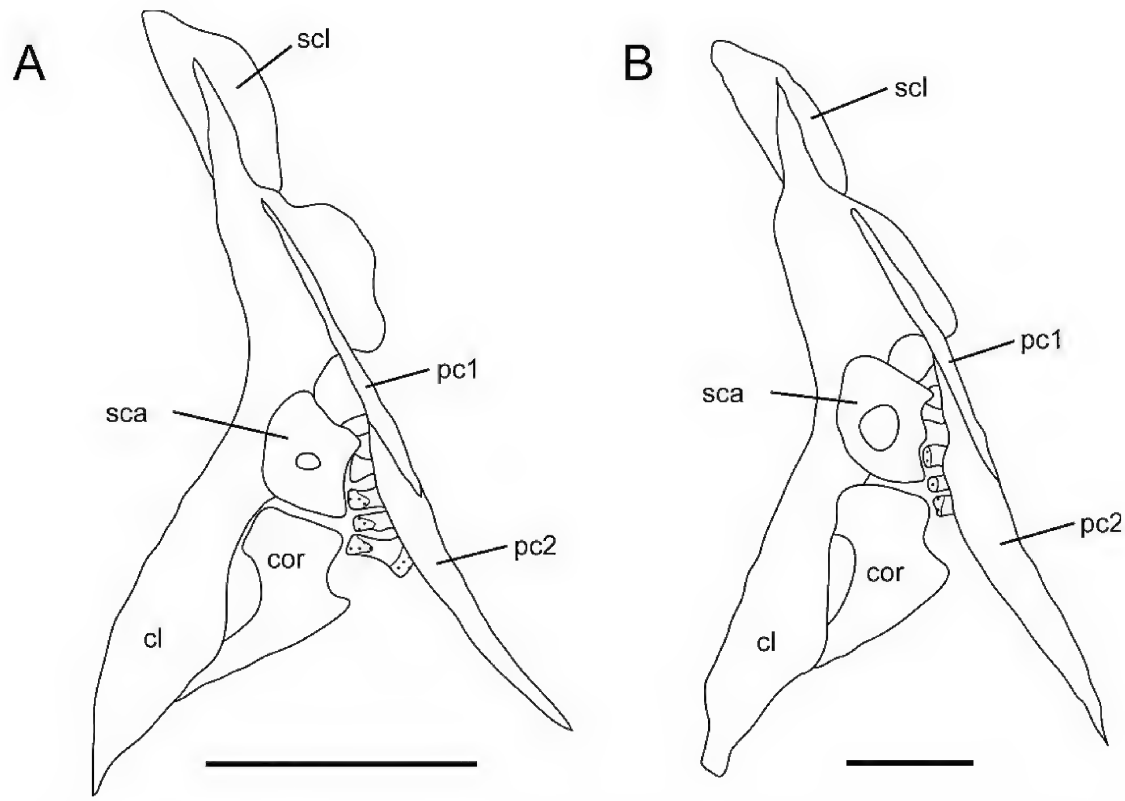


Fig. 17. Right pectoral girdle in medial view: **A,** *Ptychochromis grandidieri*, UMMZ 237312, C&S. **B,** *Paretroplus menarambo*, UMMZ 235014, C&S. Scale bars = 5 mm.

In all other cichlid genera examined an entopterygoid flange is lacking (fig. 15A). (1.00)

41. *Entopterygoid and metapterygoid suture.*

0: Considerable overlap of entopterygoid and metapterygoid, with no dorsal gap (fig. 15A).
1: Wide dorsal gap between entopterygoid and metapterygoid, with fingerlike projections or interdigitations on opposing margins of each bone (fig. 15B).

State one is unique to Etroplinae. In Etroplinae, there is little, if any, overlap of the entopterygoid and the metapterygoid; any contact between the entopterygoid and metapterygoid is confined to the ventral margin of the entopterygoid. (1.00)

42. *Entopterygoid and ectopterygoid broadly associated, little or no contact of entopterygoid and palatine.*

0: Absent.
1: Present.

In taxa exhibiting state one, there is extensive contact between the entopterygoid and ectopterygoid, but very little, if any, contact of the entopterygoid with the palatine (fig. 15B). Within Cichlidae, state one is present in the Malagasy genera *Paretroplus* and *Ptychochromis*, the central African genus *Heterochromis*, and the Neotropical genus *Retroculus* and Neotropical geophagines. In these taxa, the ectopterygoid is in contact with the palatine. In the South Asian genus *Etroplus*, the entopterygoid, not the ectopterygoid, is more broadly associated with the palatine. In other cichlid genera examined, both the ectopterygoid and entopterygoid make considerable contact with the palatine (fig. 15A). (0.33, 0.71)

43. *Symplectic morphology.*

0: Symplectic simple, long and rodlike, with smooth caudal surface (fig. 15A).

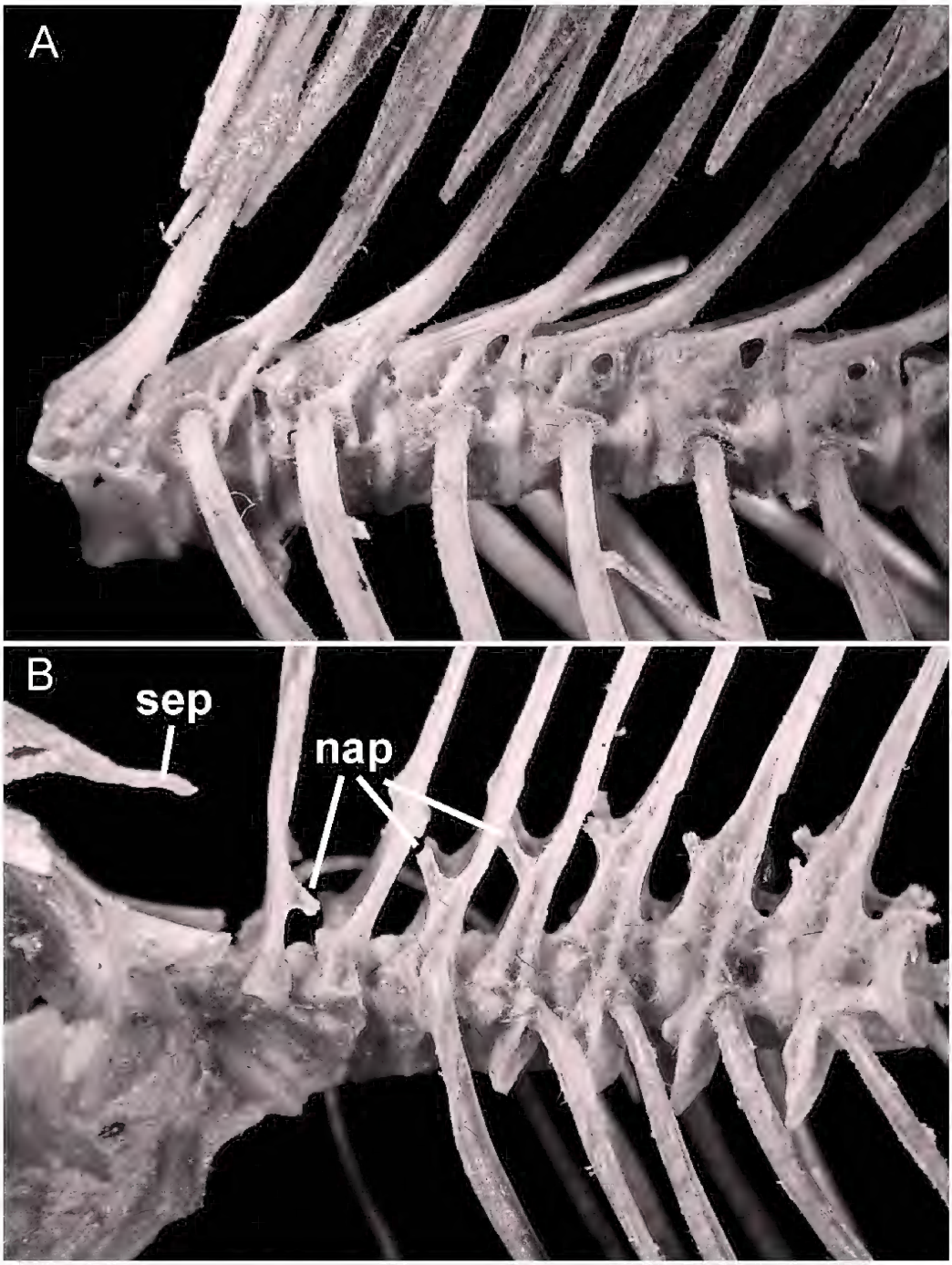


Fig. 18. Anterior vertebrae in left lateral view illustrating modified prezygopophyses on anterior neural arches in Eutroplinae: **A,** *Paratilapia* sp., UMMZ 240366, S. **B,** *Paretroplus menarambo*, UMMZ 233522, S. **C,** *Katria katria*, UMMZ 240358, C&S. **D,** *Paretroplus polyactis*, UMMZ 239527, C&S. Anterior is to the left.

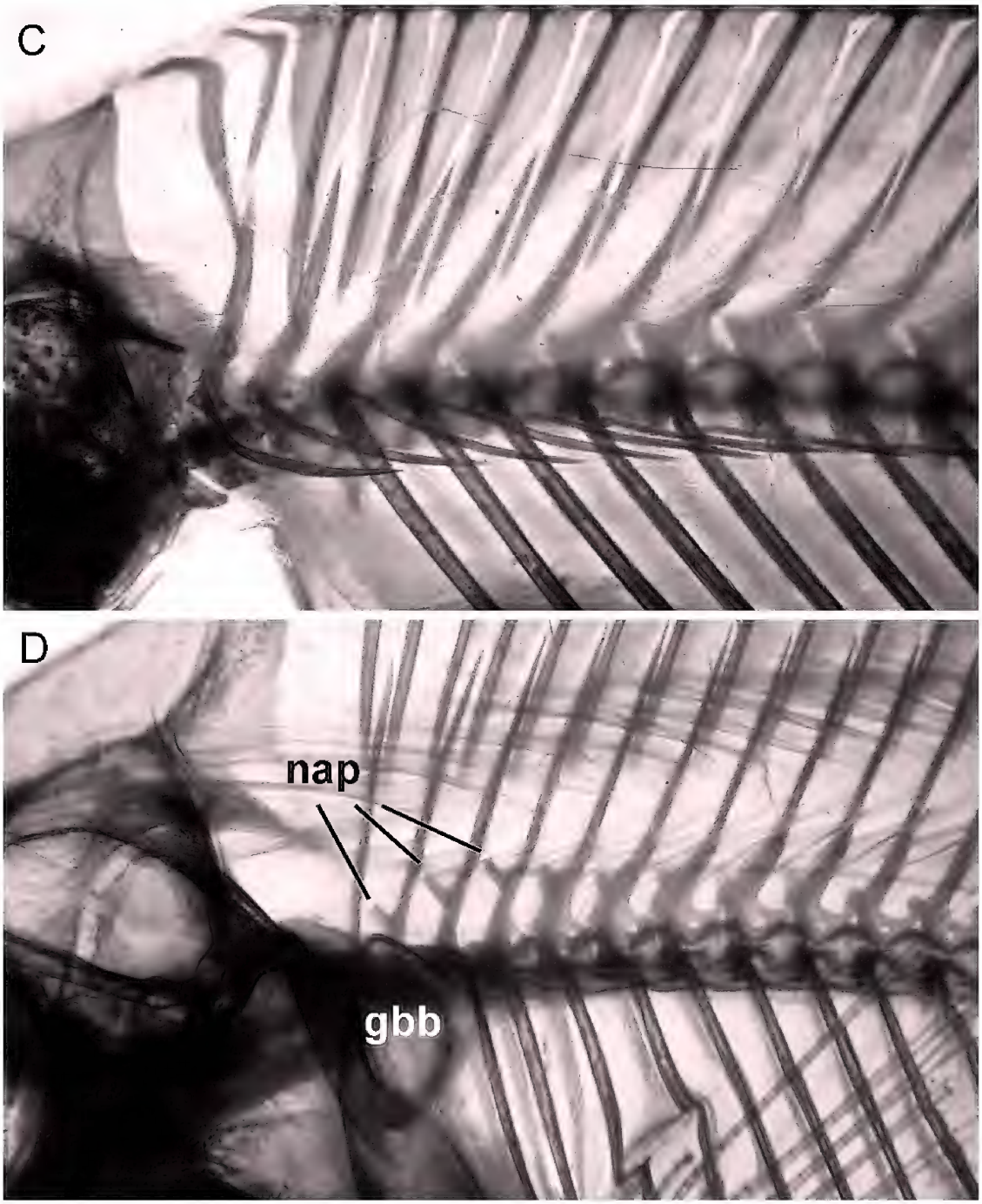


Fig. 18. Continued.

1: Symplectic complex, with well-developed spines and projections present along ventrocaudal margin (fig. 15B).

Within Cichlidae, a symplectic characterized by numerous ventral projections is unique to Etroplinae. (1.00)

44. *Apposition of symplectic and preopercle.*

0: Preopercular spine articulates with, or is very closely apposed to, symplectic; bones overlap in lateral view (fig. 15A; note: in illustration preopercular spine overlaps with dorsal portion of symplectic).
1: Symplectic and preopercular spine (or if spine is lacking, the preopercle) not in contact; gap present between bones in lateral view (fig. 15B).

A gap between the symplectic and preopercular spine is restricted to the Malagasy genera *Paretroplus* and *Oxylapia*, the latter genus being polymorphic for this feature. (1.00)

Pectoral Girdle

45. *Ventral margin of cleithrum.*

0: Tapered and/or pointed (fig. 17A).
1: Ventral margin of cleithrum (i.e., near symphysis) not tapered, but squared off, broad, flattened, and peglike ventrally (fig. 17B).

Within Cichlidae, a ventrally broad and peglike cleithrum is restricted to Etroplinae. (1.00)

Axial Skeleton

46. *Anterior neural arch processes.*

0: Prezygopophyses unmodified, located proximal to vertebral centra (figs. 10A and 18A, C).
1: Well-developed, paired, anterodorsally projecting prongs or processes, which are widely separated from the vertebral centrum and originate on anterior margin of second neural arch, present on dorsal margin of anterior neural arches; processes articulate with posterior margin of preceding neural spine, and apparently lend support to neural spines (figs. 10B and 18B, D).

State one is restricted to Etroplinae. These neural arch processes are more pronounced in *Paretroplus* than *Etroplus*. Presumably these distally situated neural arch processes represent highly modified prezygopophyses, although in some members of Etroplinae it appears as though unmodified prezygopophyses proximal to the vertebral centrum are present as well. These modified prezygopophyses (= accessory processes) are particularly well developed anteriorly, and become less pronounced and more proximal to the vertebral column posteriorly (fig. 18D). (1.00)

47. *Anterior neural arches enlarged and widened.*

0: Absent.
1: Present.

State one is restricted to Etroplinae. Members of Etroplinae are characterized by anterior neural arches that are markedly enlarged, and in which the dorsal surfaces of the anterior vertebral centra are also expansive and flattened (figs. 10B and 18B). In all other genera examined, the anterior neural arches are neither enlarged nor widened (fig. 18A). (1.00)

48. *Anterior hemal spines anteroposteriorly expanded.*

0: Anterior hemal spines not anteroposteriorly expanded (fig. 19A, B).
1: First through fifth anterior hemal spines with anteroposteriorly oriented laminar expansions, which may connect or "interlock" (fig. 19C).

In taxa exhibiting state one, the anteroposteriorly expanded hemal spines appear platelike or bladelike in lateral view. State one is present in Etroplinae, and has also been reported in other deep-bodied cichlid lineages (e.g., the Neotropical genera *Pterophyllum* and *Symphysodon*) (Sparks, 2001). (1.00)

49. *Anterior anal-fin pterygiophores insert into slots formed by laminar expansion of anterior hemal spines.*

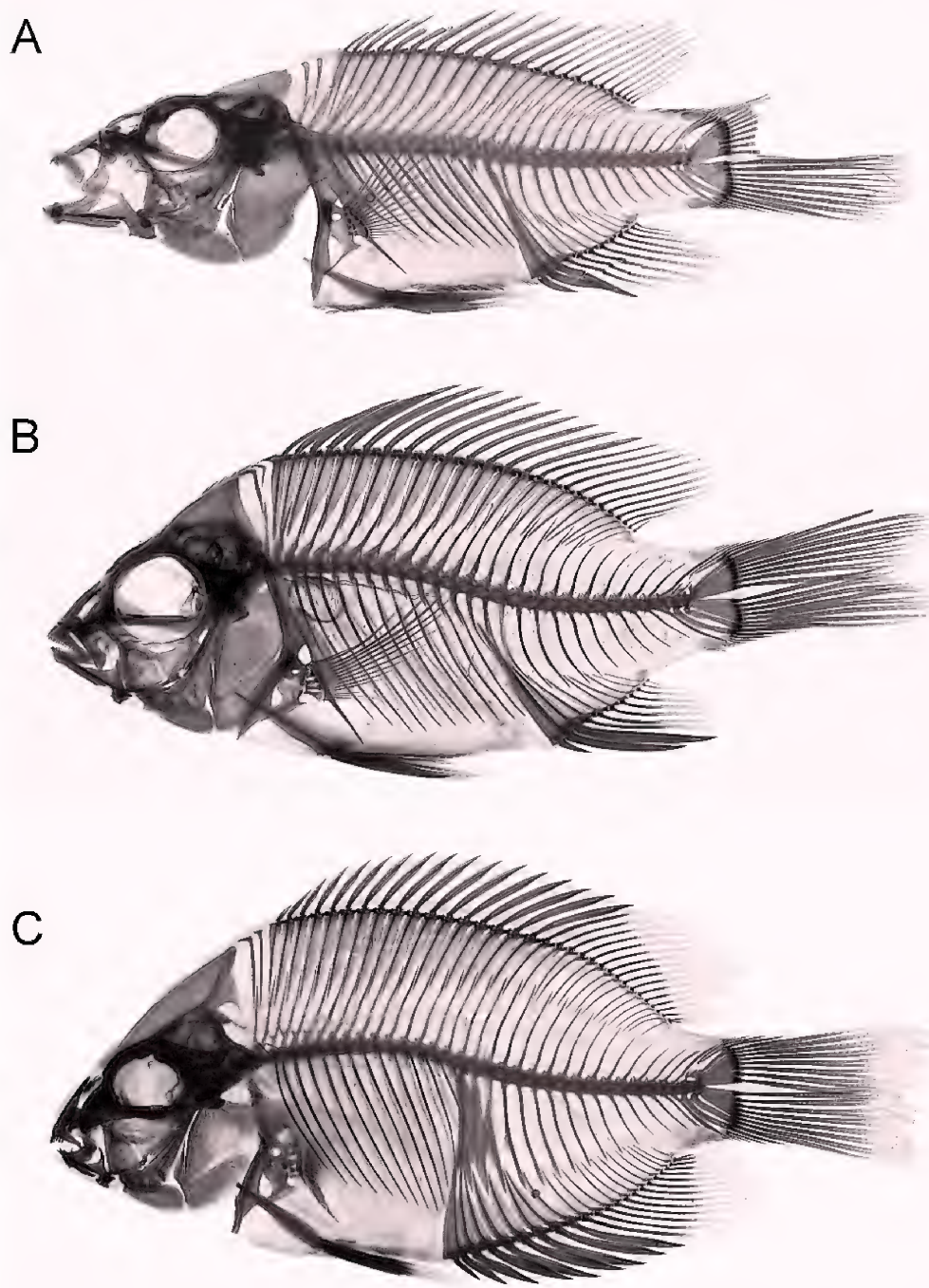


Fig. 19. Representative cleared-and-stained Malagasy cichlids: **A,** *Paratilapia polleni*, UMMZ 235043. **B,** *Ptychochromis grandidieri*, UMMZ 237312. **C,** *Paretroplus polyactis*, UMMZ 235016.

0: Absent.
1: Present.

In taxa exhibiting state one, the anterior anal-fin pterygiophores insert into slots formed by paired, anteroposteriorly oriented, laminar expansions of the anterior hemal spines (fig. 19C). State one is found in all members of Etroplinae and has also been reported in the deep-bodied Neotropical genus *Symphysodon* (Sparks, 2001). (1.00)

50. *Orientation of anterior anal-fin pterygiophores and hemal spines.*

0: Anterior anal-fin pterygiophores and hemal spines not compressed; pterygiophores dorsorostrally directed (fig. 19A, B).
1: Anterior anal-fin pterygiophores and hemal spines markedly compressed (due to presence of paired caudal extensions of gas bladder and gut), and anterior anal-fin pterygiophores dorsocaudally directed instead of dorsorostrally as in most cichlids (fig. 19C).

State one is present in Etroplinae and has also been reported in other extremely deep-bodied cichlids, including the Neotropical genera *Pterophyllum* and *Symphysodon* (Sparks, 2001). In members of Clade F (*P.* "lamena" clade), comprising *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, which are shallow-bodied riverine cichlids, the anterior anal-fin pterygiophores are only slightly dorsocaudally oriented. In all other cichlids, the anterior anal-fin pterygiophores are dorsorostrally oriented (fig. 19A, B). (1.00)

51. *Anteriormost caudal vertebral centra bearing accessory parapophyses* (Stiassny et al., 2001).

0: Accessory parapophyses absent on caudal vertebral centra (fig. 19A, B).
1: Accessory parapophyses present on anterior 1–5 caudal vertebral centra (Stiassny et al., 2001: fig. 5) (fig. 19C).

Stiassny et al. (2001) define the first caudal vertebra as the first centra through which the caudal artery enters a closed hemal canal, and which usually bears a single median hemal spine, and this interpretation is followed here. State one is present in Etroplinae, and has also been reported in the deep-bodied Neotropical genera *Pterophyllum* and *Symphysodon* (Sparks, 2001). Although Stiassny et al. (2001: fig. 5) report that accessory parapophyses are lacking in *Etroplus*, I find these structures present on the anteriormost caudal vertebral centra in all three species of *Etroplus*. Accessory parapophyses are present on the anteriormost 2–5 caudal vertebral centra in *Paretroplus* (fig. 19C). The anteriormost parapophyses (= those present on the first caudal vertebra) bear reduced ribs in some species examined (e.g., *P. polyactis*, *P. dambabe*), whereas accessory parapophyses on subsequent vertebral centra have no associated ribs. These structures appear to lend support to the upper margins of the paired posterior gas bladder chambers in members of Etroplinae. (1.00)

52. *Distribution of accessory parapophyses on caudal vertebral centra.*

0: Accessory parapophyses present only on first caudal vertebral centra (*Etroplus*).
1: Accessory parapophyses present on first two caudal vertebral centra (Clade F, *Paretroplus* "lamena" clade).
2: Accessory parapophyses present on the anteriormost 3–5 caudal vertebral centra (remaining members of *Paretroplus*).

Accessory parapophyses are restricted to the anteriormost caudal vertebral centra in *Etroplus* (state 0), to the first two caudal vertebral centra in *Paretroplus damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe* (state 1), and are present on the first three to first five caudal centra in the remaining species of *Paretroplus* (state 2), except *P. polyactis*. *Paretroplus polyactis* (coded as polymorphic for this feature) generally has accessory parapophyses restricted to the first two caudal vertebral centra, but these structures are occasionally also present on the third caudal centra. *Paretroplus kieneri* has accessory parapophyses present on the anterior three caudal vertebral centra, *P. dambabe* on the first three or four caudal vertebral centra, and *P. maromandia*, *P. maculatus*, and *P. menarambo* on the first four or five caudal vertebral centra. As mentioned above, these parapophyses directly support the upper wall of the paired posterior gas bladder chambers. (1.00)

53. *Asymmetrical displacement of first and second anal-fin pterygiophores* (Stiassny et al., 2001).

0: Absent.
1: Present.

State one is restricted to the South Asian genus *Etroplus* in which there is an asymmetrical displacement of first anal-fin pterygiophore to the left and the second to the right of the hemal spine complex (Stiassny et al., 2001: fig. 4). Rarely, the reverse configuration occurs in which the first anal-fin pterygiophore is displaced to the right and the second to the left of the hemal spine complex (personal obs.), although this feature (i.e., displacement of the first anal-fin pterygiophore either to the left or right) is still unique to *Etroplus*. (1.00)

54. *Supraneural (= predorsal) bones L-shaped.*

0: Absent.
1: Present.

In taxa exhibiting state one, two supraneural (= predorsal) bones are present with elongate procurrent processes on each, such that the supraneural bones resemble inverted L's; no posteriorly directed process is present on either predorsal element (fig. 10A) (Sparks and Reinthal, 2001). State one is restricted to the ptychochromin genera *Ptychochromis*, *Ptychochromoides*, and *Oxylapia*. Although the procurrent processes are frequently variably and poorly developed in juvenile *Oxylapia*, they are well developed in large adults. (1.00)

55. *First dorsal-fin pterygiophore with well-developed procurrent spine* (Cichocki, 1976; Reinthal and Stiassny, 1997; Sparks and Reinthal, 2001).

0: Absent.
1: Present.

A prominent procurrent spine is present on the first dorsal-fin pterygiophore in the ptychochromin genera *Ptychochromis*, *Ptychochromoides*, and *Oxylapia* (fig. 10A). In all other genera examined for this study, a procurrent spine on the first dorsal-fin pterygiophore is lacking (fig. 10B); however, a procurrent spur is present in the South American genus *Gymnogeophagus* (Gosse, 1976; Cichocki, 1976; Reinthal and Stiassny, 1997; Sparks and Reinthal, 2001; Stiassny and Sparks, 2006). (1.00)

Median Fins and Fin Supports

56. *Anal-fin spine number elevated, and several anterior pterygiophores associated with first hemal spine* (Cichocki, 1976: 168).

0: Anal-fin spine count not elevated (i.e., generally 3–4) (fig. 19A, B).
1: Anal-fin spine count 7–10, several anterior pterygiophores associated with first hemal spine (fig. 19C).
2: Ten or greater (generally 12–14) anal-fin spines, several anterior pterygiophores associated with first hemal spine.

State one is present in the Malagasy genus *Paretroplus*, and has also been reported in the Neotropical genus *Symphysodon* and *Archocentrus nigrofasciatus* (Sparks, 2001). State two is unique to the South Asian genus *Etroplus*. (1.00)

Gas Bladder

57. *Paired anterior gas bladder extensions.*

0: Absent.
1: Present.

Paired anterior gas bladder extensions are present in all of the Malagasy–South Asian cichlids, although the development, complexity, and anterior reach of these chambers vary considerably (compare fig. 10A with fig. 20). Although anterior gas bladder extensions of some form are present in almost all cichlids, they seldom extend much anterior of the first pleural ribs (e.g., fig. 10A). Apart from the Malagasy–South Asian lineages paired anterior gas bladder extensions are most pronounced in the Neotropical genera *Chaetobranchopsis* and *Geophagus*, and the Central African genus *Heterochromis*. (Uninformative in current analysis)

58. *Anterior limit of paired anterior gas bladder extensions.*

0: Paired anterior gas bladder extensions extend just anterior of first pleural ribs,

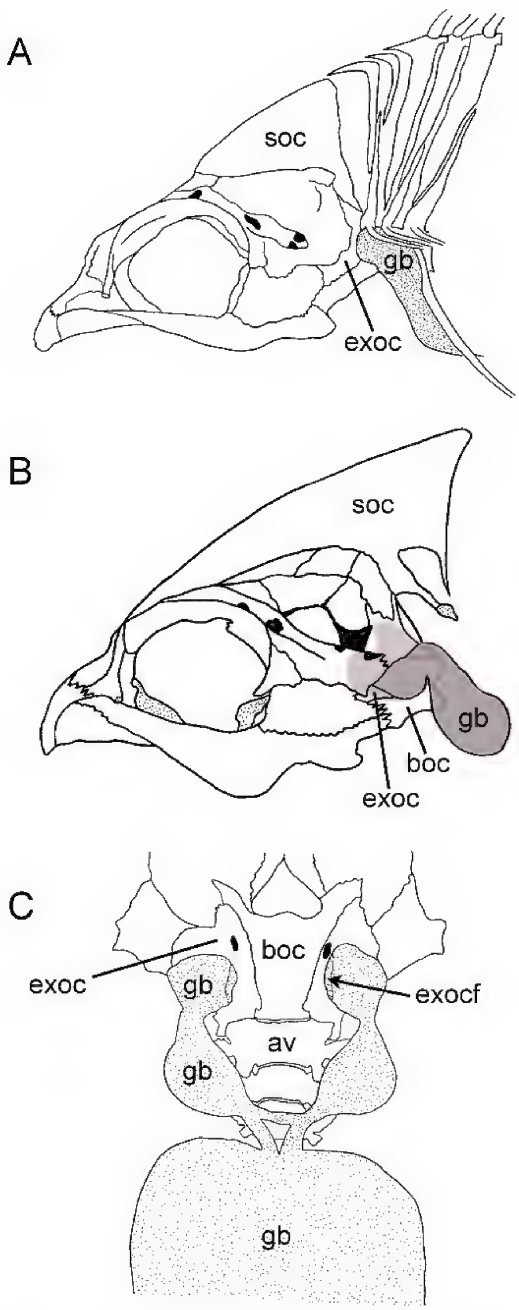


Fig. 20. Morphology of anterior gas bladder extensions and relationship to neurocranium. Lateral view of otophysic connection in representative member of: A, Ptychochrominae (*Ptychochromis inornatus*, UMMZ 237064, 88.0 mm SL, C&S) in which gas bladder horns abut neurocranium; B, Etroplinae (*Paretroplus polyactis*, UMMZ 235016, 65.0 mm SL, C&S) in which complex rostral gas bladder diverticula (darker shading) penetrate exoccipital and expand into large bullae (lighter shading) in direct contact with labyrinth. C, Ventral view of anterior gas bladder-neurocranial linkage (stippled) in *Paretroplus* (*P. nourissati*, UMMZ 235206, 67.0 mm SL, C&S). Arrow indicates exoccipital foramina through which gas bladder bullae penetrate skull, however, extent of intracranial bullae are not shown.

but do not approach exoccipital region of skull (fig. 10A).
1: Paired anterior gas bladder extensions contact, or very nearly contact, exoccipitals (fig. 20A–C).

State one is present in all of the Malagasy–South Asian cichlids, less *Katria* and *Oxylapia*. In taxa exhibiting state one, if the anterior gas bladder extensions do not directly contact the skull, they are closely associated with the exoccipital region via connective tissue. In the central African genus *Heterochromis*, paired anterior extensions extend to about the level of articulation of the vertebral column and the neurocranium, but they do not approach the exoccipitals. Narrow paired anterior extensions that extend relatively far anteriorly are also present in the Neotropical genus *Chaetobranchopsis*, but there is a wide gap between their anterior limit and the rear of the skull. (0.33, 0.00)

59. *Paired anterior gas bladder extensions extend into exoccipital foramina.*

0: Absent.
1: Present.

In taxa exhibiting state one, paired anterior gas bladder extensions extend into enlarged exoccipital recesses, either partially or fully (fig. 20B, C). State one is present in the Malagasy genus *Paratilapia*, where the anterior gas bladder extensions extend only partially into the exoccipital recesses but do not expand within these foramina (i.e., do not fill the exoccipital chambers), and Etroplinae, where rigid anterior gas bladder bullae expand into enlarged exoccipital recesses, within which they are securely lodged (Character 60) (fig. 20B, C). (1.00)

60. *Paired anterior gas bladder bullae firmly lodged in and expanded within exoccipital recesses.*

0: Absent.
1: Present.

State one is restricted to members of Etroplinae. In Etroplinae the gas bladder extends through an enlarged exoccipital foramina and expands into a large bulla that is in direct contact with the labyrinth, thus forming a direct mechanical (= otophysic) connection between the gas bladder and inner ear (fig. 20B, C). These paired anterior gas bladder extensions, found in all members of Etroplinae, are firmly lodged in and expanded within uniquely enlarged and complex exoccipital foramina (Character 14). *Paratilapia* is the only other cichlid genus in which anterior gas bladder extensions have been observed to penetrate the exoccipital foramina; however, in *Paratilapia* the gas bladder does not expand into these foramina (i.e., narrow paired anterior extensions only slightly enter the neurocranium and are not in direct contact with the margins of the exoccipital foramina). (1.00)

61. *Paired anterior gas bladder bullae "polyp-like" with extremely narrow connections to main chamber* (Cichocki, 1976; Stiassny et al., 2001).

0: Absent.
1: Present.

In *Paretroplus* the anterior gas bladder extensions are complex and characterized by multiple anterior polyplike (= teardrop shaped) chambers or bullae, with extremely narrow connections (= diverticula) to the main gas bladder chamber (fig. 20B, C). In all other genera with anterior gas bladder extensions, these chambers are simple tubes with wide connections to the main chamber of the gas bladder (figs. 10A and 20A). (1.00)

62. *Anterior gas bladder bullae with tough and thickened tunica externa.*

0: Absent.
1: Present.

In *Paretroplus* the anterior, polyplike, gas bladder chambers (= bullae) exhibit a tough, thickened, and rigid tunica externa, which is "rubbery" and difficult to rupture, even with a sharp scalpel (fig. 20B, C). In all other cichlids with paired anterior projections of the gas bladder, the tunica externa is feeble and easily penetrated (figs. 10A and 20A). (1.00)

63. *Caudal extensions of gas bladder deep bodied, anterior hemal spines and anal-fin pterygiophores compressed* (Cichocki, 1976: 169).

0: Absent.
1: Present.

In taxa exhibiting state one, the paired caudal gas bladder extensions are deep-bodied, and there is associated compression of both the anterior hemal spines (especially the first and second, proximal to their origin) and anal-fin pterygiophores (fig. 19C). This configuration is present only in Etroplinae, where these posterior gas bladder chambers may extend from the 3rd to 6th hemal spine depending on species. Deep-bodied caudal extensions of the gas bladder have also been reported in the Neotropical cichlids *Chaetobranchopsis australis* and *Archocentrus nigrofasciatus*, except in these taxa there is no accompanying compression of the anterior hemal spines. (1.00)

Laterosensory System

64. *Laterosensory canal system on the mandible, preopercle, and neurocranium characterized by markedly enlarged canals and expanded pores* (Sparks, 2004a).

0: Laterosensory canals not enlarged and pores not expanded (figs. 4C–D, 10B, and 16A, C–E).
1: Laterosensory canals on head markedly enlarged and pores greatly expanded (figs. 4A–B, 10A, and 16B).

State one is present in all members of the Malagasy genus *Ptychochromis* (fig. 4B; Stiassny and Sparks, 2006: fig. 5), the Malagasy species *Katria katria* (fig. 10A), and the monotypic central African genus *Heterochromis* (figs. 4A and 16B). (0.50, 0.66)

Fig. 21. External anatomy illustrating characteristic external features of included genera: **A,** *Ptychochromoides vondrozo*, holotype, UMMZ 235297, 182.0 mm SL. **B,** *Ptychochromis inornatus*, holotype, UMMZ 237492, 115.3 mm SL. **C,** *Etroplus suratensis*, AMNH 217756, 146.2 mm SL. **D,** *Paretroplus menarambo*, UMMZ 235014, 161.7 mm SL.

External Morphology and Squamation

65. *Snout morphology.*

> 0: Comparatively elongate and pointed (fig. 21A–B).
> 1: Blunt and rounded, profile steeply sloping (fig. 20C–D).

State one is unique to Clade J, comprising all of the deep-bodied members of *Paretroplus* (*P. petiti*, *P. menarambo*, *P. maromandia*, *P. dambabe*, and *P. maculatus*) (fig. 21D), less *P. polyactis*, and to the South Asian species *Etroplus suratensis* (fig. 21C) and *E. canarensis*. Although the snout is similarly blunt in smaller specimens of both *E. suratensis* and *E. canarensis* (< about 75 mm SL), it becomes more elongate and pointed with increasing size. In contrast, in deep-bodied members of *Paretroplus*, the snout remains blunt regardless of standard length. (0.50, 0.83)

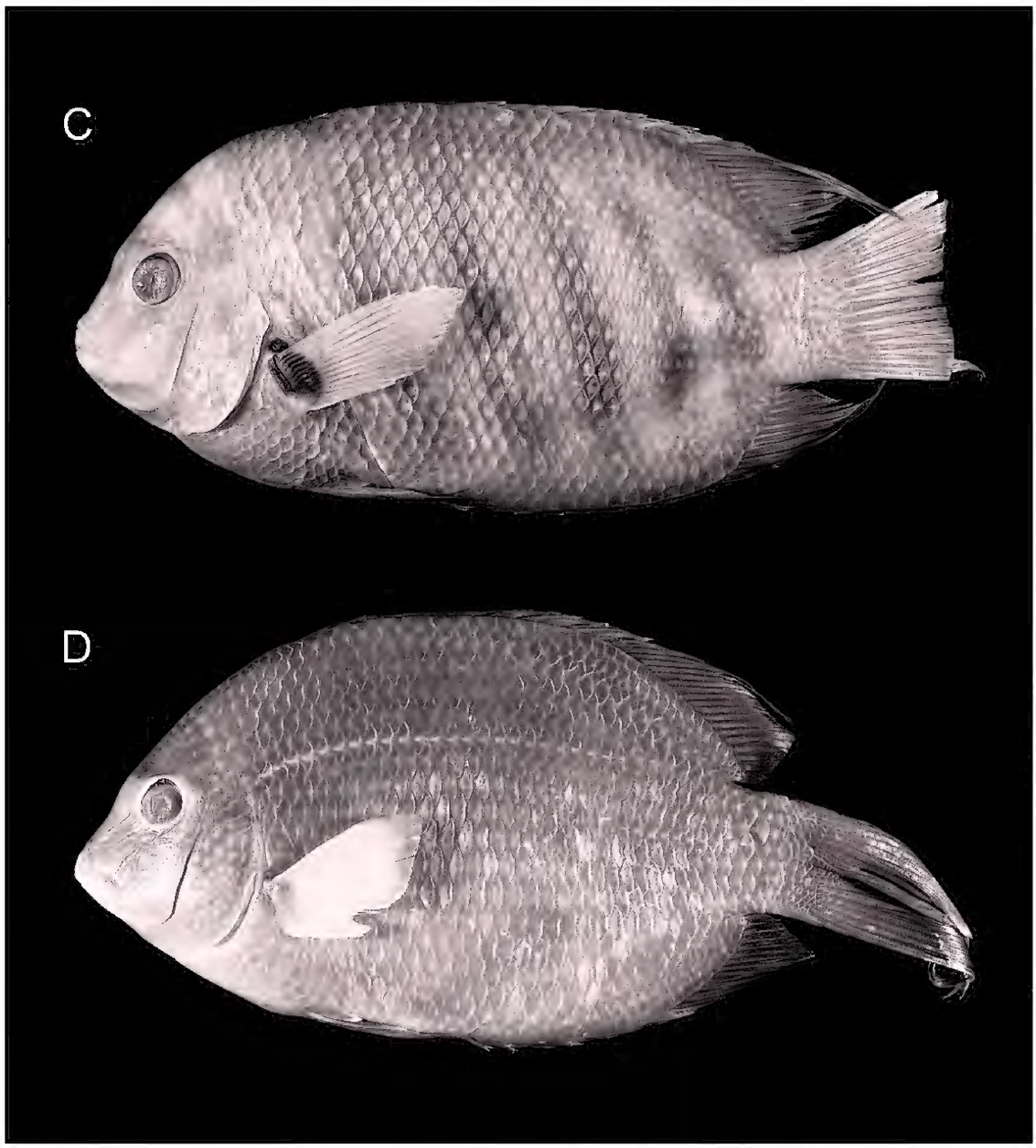


Fig. 21. Continued.

66. *Body very deep and essentially disk-shaped.*

0: Absent.
1: Present.

A deep, disk-shaped body is restricted to members of Clade I (i.e., *Paretroplus polyactis*, *P. menarambo*, *P. petiti*, *P. maculatus*, *P. maromandia*, and *P. dambabe*) (figs. 19C and 21D), which comprise the deep-bodied clade of Sparks (2004a) and Sparks and Smith (2004). A deep, disk-shaped body is also present in the Neotropical genera *Pterophyllum* and *Symphysodon* (not included in phylogenetic analysis). (1.00)

67. *Well-developed lateral ridges of scales or "scale sheathing" along the bases of the dorsal and anal fins* (Cichocki, 1976).

0: Absent.
1: Present.

State one is unique to Etroplinae. In members of Etroplinae the scale ridges are either separated from or weakly connected to the dorsal- and anal-fin bases via a membrane (i.e., they can be pulled away from the fins intact) (fig. 22). These scale ridges form a distinct furrow into which the anal and dorsal fins may partially retract, and are more prominent and more well developed anteriorly on both fins. In all other cichlid genera examined, scale ridges are lacking (e.g., fig. 21A–B). (1.00)

68. *Lateral ridges of scales ("scale sheathing") free from fin membranes over entire length of soft dorsal and anal fins.*

0: Absent.
1: Present.

In taxa exhibiting state one, the lateral ridges of scales ("scale sheathing", Character 67) characteristic of Etroplinae are free from the soft dorsal- and anal-fin membranes over their entire length (fig. 22A). Although the scale ridges become more tightly attached to the fin membranes posteriorly, they remain detached dorsally and do not become completely fused to the fin membranes as in other members of *Paretroplus* (e.g., fig. 22B). State one is unique to members of Clade I, the deep-bodied clade of *Paretroplus* (*P. petiti*, *P. menarambo*, *P. maromandia*, *P. dambabe*, *P. maculatus*, and *P. polyactis*). In the South Asian species *Etroplus suratensis*, the scale ridges are mostly free from the fin membrane on the anal fin, but not on the dorsal fin (fig. 21C). (1.00)

69. *Pelvic axillary scale well developed.*

0: Absent.
1: Present.

Within Cichlidae, a well-developed, large pelvic axillary scale is present only in Etroplinae (figs. 22A and 23) and the Neotropical genus *Cichla* (not included in phylogenetic analysis), where it is somewhat less well developed (Sparks, 2001). In all other cichlid genera examined, a well-developed pelvic axillary scale is lacking (e.g., fig. 21A–B). (1.00)

70. *Posterior field of flank scales.*

0: Posterior field well ossified (fig. 23A–B).
1: Posterior field (= caudal margin) of body scales very thin, effectively creating an unossified "flap" (fig. 23C).

In taxa exhibiting state one, the posterior margin of the body scales is not ossified, lacks circuli, and is somewhat extended (appearing triangular in lateral view) (figs. 22B and 23C). This unossified "flap" is mostly translucent, and easily detected as it protrudes out from the body and curls up when the external surface of the specimen becomes desiccated. State one is unique to members of Clade E, comprising *P. damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe*. (1.00)

71. *Interpelvic scale series well developed.*

0: Absent.
1: Present.

In taxa exhibiting state one, the interpelvic "scale", which is frequently comprised of a series of elongate scales, is well developed and extended. Among the Malagasy–South Asian cichlids state one is unique to Etroplinae, however, a similar condition is reported to occur in a number of other cichlid lineages (Sparks, 2001), none of which are included here in the phylogenetic analyses. (1.00)

72. *Squamation extends onto soft dorsal and anal fins.*

0: Absent.
1: Present.

In taxa exhibiting state one, multiple discrete rows of scales extend well beyond the scale ridges (Character 67) and onto both the soft dorsal and anal fins, and are confined to the membranes between the fin rays (fig. 22B). State one is restricted to members of Clade F, comprising *P. nourissati*, *P. tsimoly*, and *P. lamenabe*. In these three

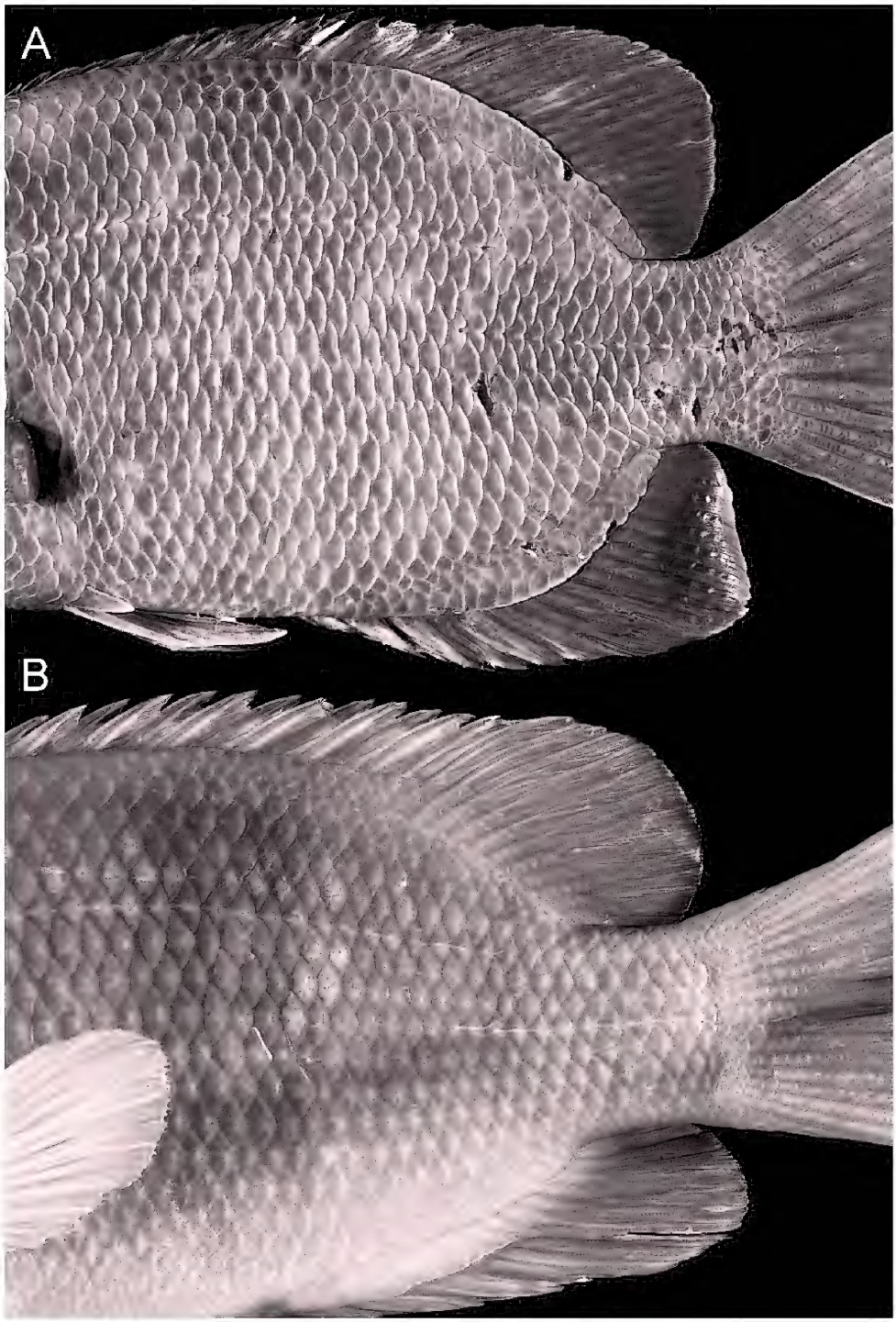


Fig. 22. Scale ridges (= scale sheathing) along dorsal- and anal-fin bases in: **A,** *Paretroplus menarambo*, AMNH 226311, 158 mm SL, in which scale ridges are free from fin membrane over entire length. **B,** *Paretroplus nourissati*, UMMZ 235206, 124.3 mm SL, in which scale ridges are fused to fin membranes posteriorly on both soft dorsal and anal fins. Anterior is to left.

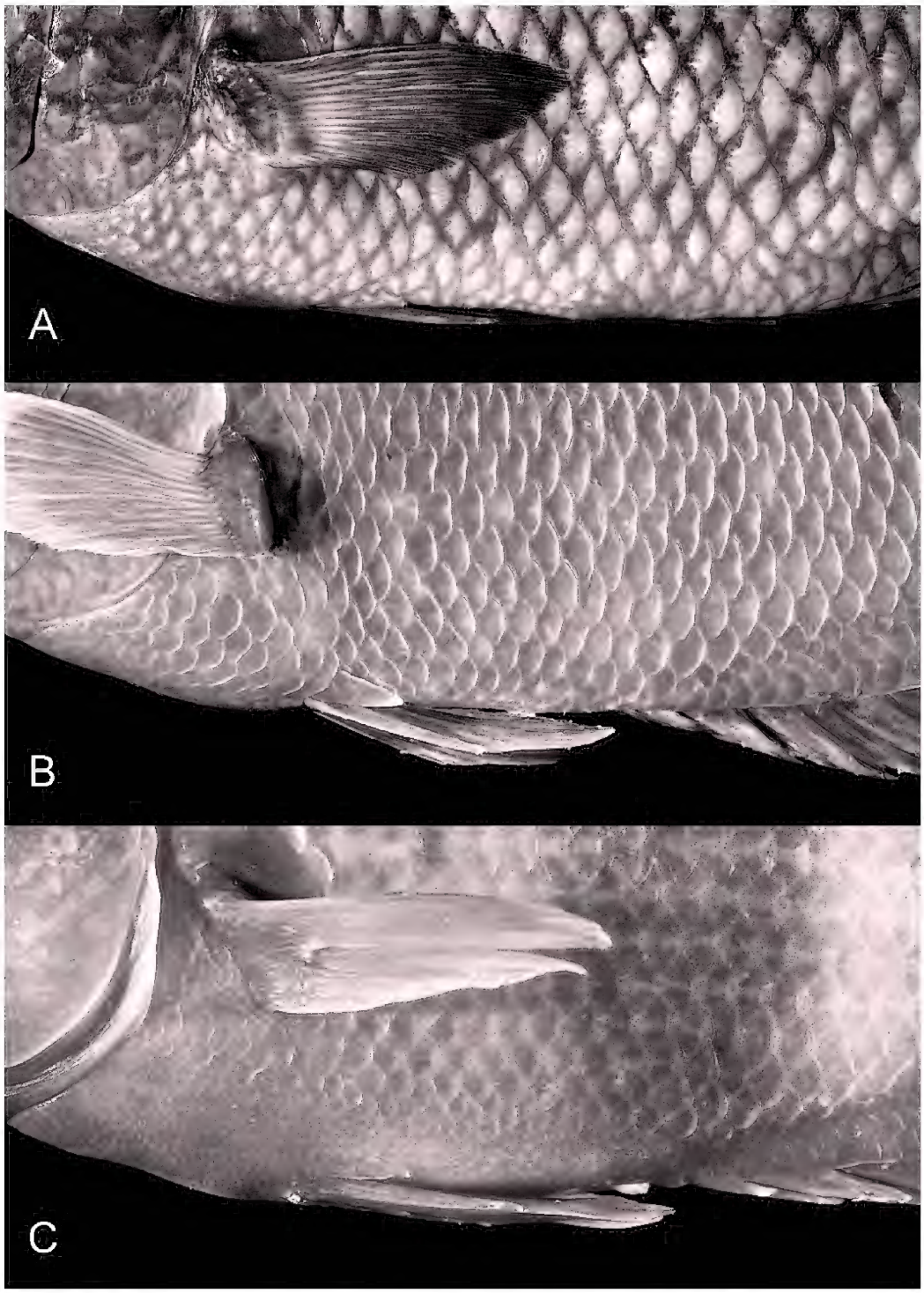


Fig. 23. Squamation pattern on ventral flank and chest in: **A,** *Paretroplus polyactis*, AMNH 88116, 189.5 mm SL. **B,** *Paretroplus menarambo*, AMNH 226311, 158.0 mm SL. **C,** *Paretroplus tsimoly*, AMNH 238563, 120.6 mm SL. Anterior is to left.

species, the characteristic scale ridges diagnostic of Etroplinae become fused and inseparable from the fin membrane posteriorly on both the soft dorsal and anal fins. Squamation on the unpaired fins is especially pronounced in *P. lamenabe*, and is not as extensive in both *P. nourissati* and *P. tsimoly*. In other members of *Paretroplus*, scales do not extend onto the fin membranes beyond the characteristic scale ridges (fig. 22A). (0.50, 0.80)

73. *Chest scales markedly reduced in size and embedded.*

0: Absent.
1: Present.

Highly embedded chest scales that are markedly reduced in size (compared to flank scales) are present in members of Clade E, comprising *Paretroplus damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe* (figs. 23C and 24C). State one is also present in the Malagasy species *Ptychochromoides vondrozo* (fig. 21A) and *Oxylapia polli*, the Neotropical genus *Retroculus*, and the central African species *Heterochromis multidens*. Compared to *Etroplus*, in which the chest scales are at most slightly reduced in size (fig. 21C), all members of *Paretroplus* exhibit chest scales of reduced size (figs. 21D and 23A–C). (0.33, 0.71)

74. *Multiple rows of scales markedly reduced in size present on the flanks dorsal to the pelvic fins and anus.*

0: Absent.
1: Present.

In taxa exhibiting state one, scales markedly reduced in size extend (several rows in depth) from the chest, continue dorsal of the pelvic fins and anus, and terminate at about anal-fin origin (fig. 23C). This condition is easy to visualize in lateral view. State one is present in members of Clade E, comprising *P. damii*, *P. nourissati*, *P. tsimoly* (including populations from the upper Kamoro River), and *P. lamenabe*. In all other species of *Paretroplus*, scales in this region are not reduced in size compared to more dorsal lateral body scales (e.g., fig. 23A–B). (1.00)

Pigmentation Pattern and Coloration

75. *Lateral horizontal striping pattern.*

0: Absent.
1: Present.

In taxa exhibiting state one, a distinctive alternating light and dark horizontal striping pattern is present on the body, and is continuous from about the anterior margin of the orbit to caudal-fin origin (fig. 24B). State one is unique to a clade of *Paretroplus* (Clade J) comprising deep-bodied members of the genus with distributions restricted to western basins (i.e., all deep-bodied species less *P. polyactis*; see Character 66), and includes *P. petiti*, *P. maculatus*, *P. menarambo*, *P. dambabe*, and *P. maromandia*. (1.00)

76. *Seven to nine prominent dark lateral bands.*

0: Absent.
1: Present.

Seven to nine lateral bands of about equal intensity are present in members of the deep-bodied *Paretroplus* clade, Clade I (i.e., *P. polyactis*, *P. maculatus*, *P. menarambo*, *P. maromandia*, and *P. dambabe*) (fig. 24A–B), except possibly *P. petiti*, which is known only from the holotype (a juvenile) and which is uniformly dark overall in preservative. Although these lateral bands are of about equal intensity within an individual, band intensity varies considerably between individuals and interspecifically, as well as ontogenetically. Although seven to nine lateral bands are always present in members of Clade I, occasionally the anteriormost band, which is located at about the level of the posterior margin of the opercle, and less frequently the posteriormost band, located on the caudal peduncle, are considerably more faint than the others. Even in these cases, the remaining bands are prominent and of about equal intensity. Seven to nine lateral bands are also present in members of the South Asian genus *Etroplus* (less *E. maculatus*) and the Neotropical genus *Retroculus*. The African species *Heterochromis multidens* possesses at most five or six lateral bands. Other species of *Paretroplus* either lack lateral banding (e.g., *Paretroplus damii*, *P. kieneri*, and *P. gymnopre-*

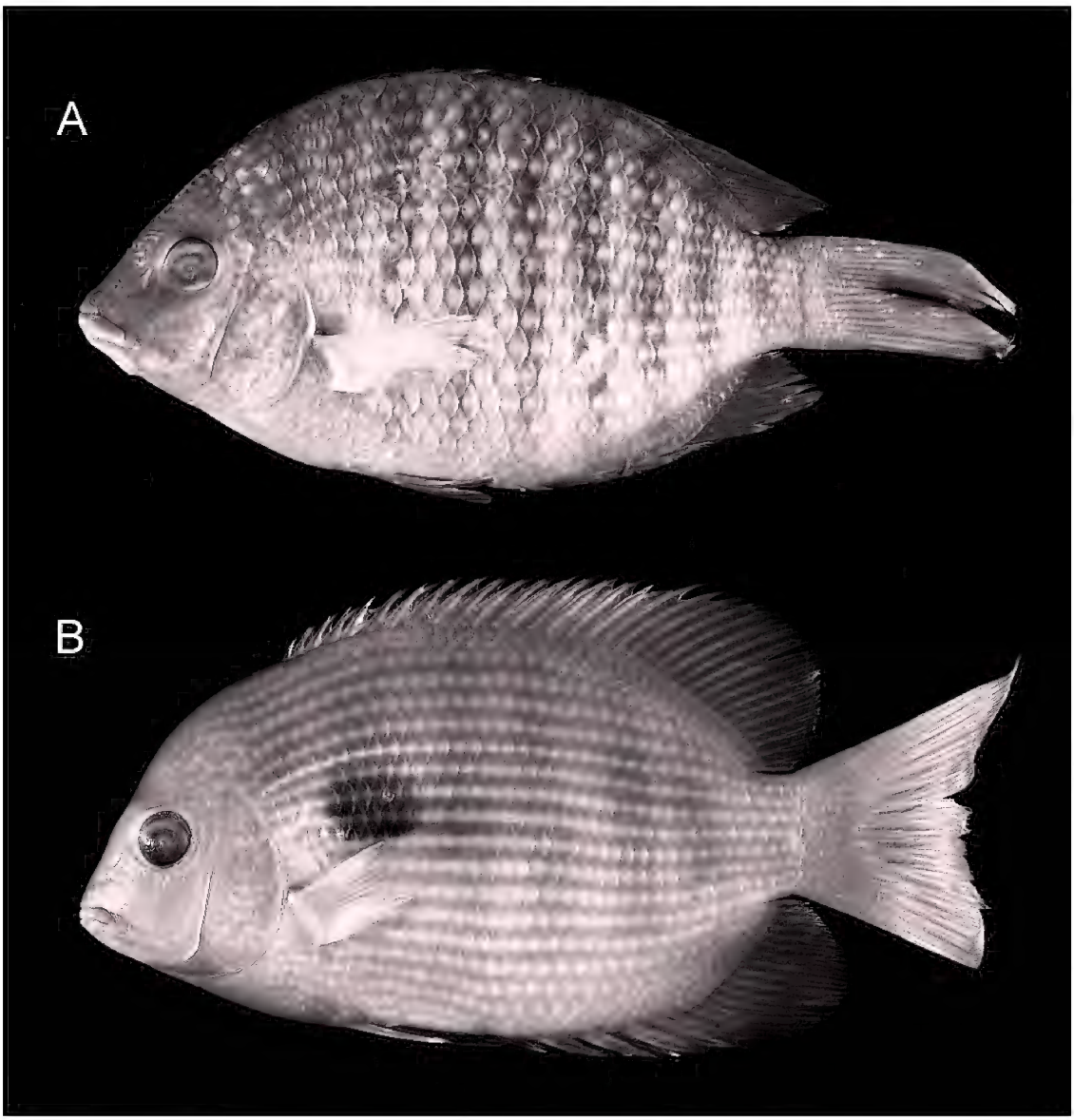


Fig. 24. Lateral pigmentation pattern in: **A,** *Paretroplus polyactis*, AMNH 238569, 99.3 mm SL, illustrating lateral banding pattern. **B,** *Paretroplus maculatus*, UMMZ 235019, 113.8 mm SL, illustrating horizontal striping pattern. **C,** *Paretroplus nourissati*, UMMZ 235206, 124.0 mm SL, illustrating two prominent and convergent midlateral bands. **D,** *Paretroplus gymnopreopercularis*, UMMZ 239531, paratype, 146.6 mm SL, illustrating blotchy and mottled pigmentation pattern and the absence of lateral banding.

opercularis; figs. 24D, 25A, 26, and 27), or if bands are present they are not roughly equal in intensity (members of Clade F; fig. 24C). (0.33, 0.71)

77. *Two wide and convergent black midlateral bands.*

0: Absent.
1: Present.

Two prominent, wide, and convergent midlateral bands are unique to members of a clade comprising *P. nourissati*, *P. tsimoly*, and *P. lamenabe* (fig. 24C). Other bands are

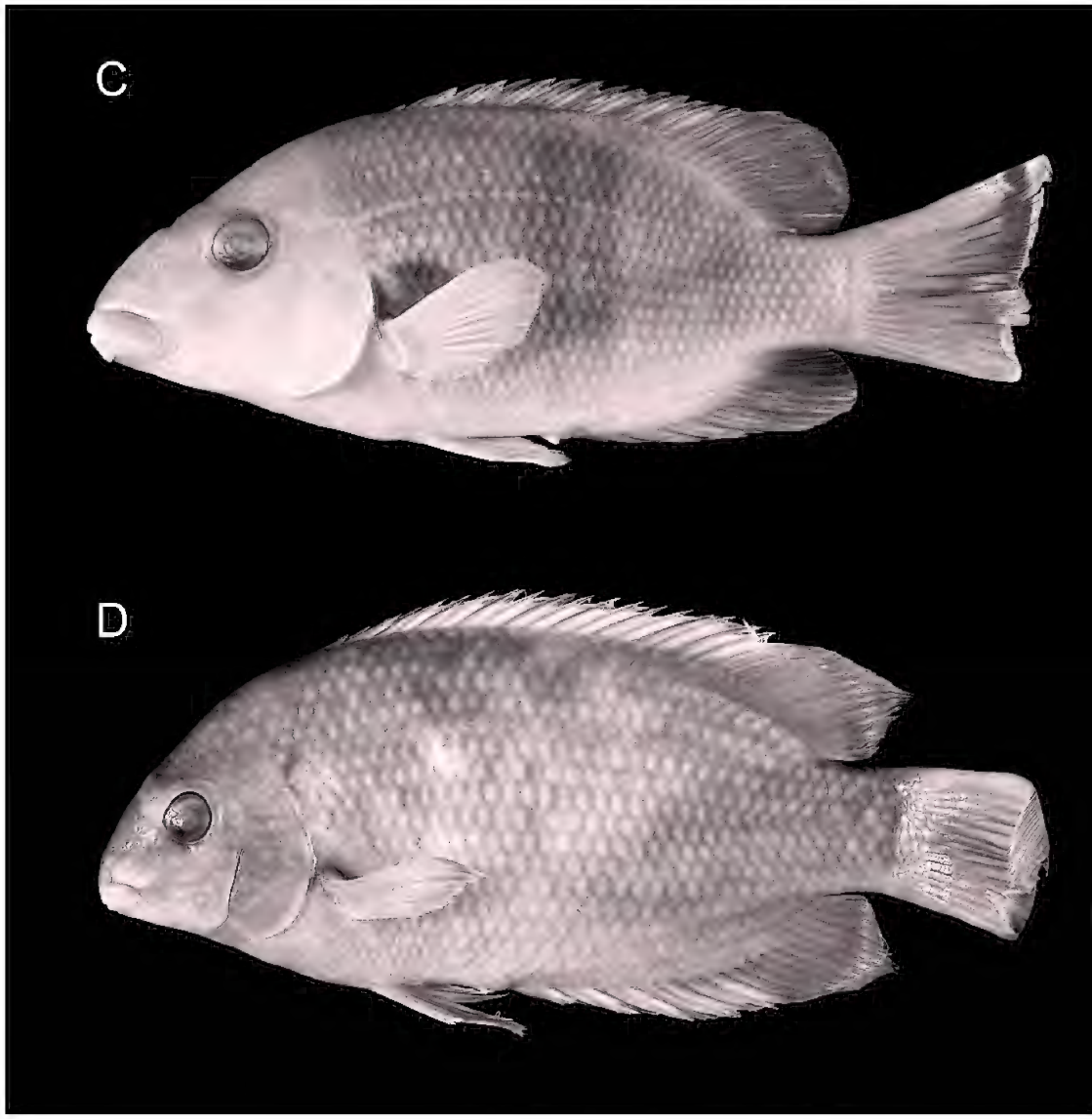


Fig. 24. Continued.

present on the flanks in these three Malagasy species, but they are much less pronounced than the two midlateral bands, which become especially prominent during breeding (see de Rham and Nourissat, 2004: 118, 122, 125, 127). (1.00)

78. *Blotchy, mottled, and speckled grayish-black or brownish overall pigmentation pattern.*

0: Absent.
1: Present.

Of the taxa examined in this study, state one is restricted to members of *Ptychochromoides* (fig. 21A) and *Oxylapia*. (1.00)

79. *Blotchy orange, gray, and brown pigmentation pattern.*

0: Absent.
1: Present.

Among the taxa examined, a blotchy orange, gray, and brown pigmentation pat-

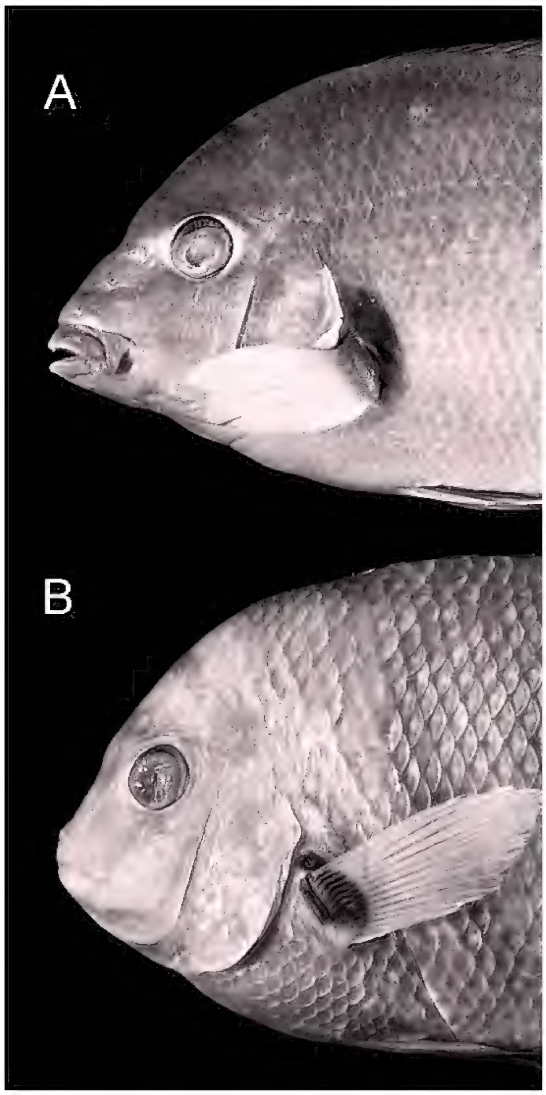


Fig. 25. Pectoral pigmentation pattern in: **A,** *Paretroplus damii*, AMNH 232461, 134.6 mm SL, illustrating prominent black pectoral-axil patch characteristic of members of Clade E. **B,** *Etroplus suratensis*, AMNH 217756, 146.2 mm SL, illustrating lateral banding pattern and black patch at base of pectoral fin.

tern is unique to *Paretroplus kieneri* and *P. gymnopreopercularis* (fig. 24D). The Malagasy name for *P. kieneri* is *kotsovato*, which refers to the rocklike coloration (*vato* = "rock" in Malagasy) of the species. These two sister species lack even faint vertical bars, which are present to some degree in all other members of the genus (e.g., fig. 24A–C). (1.00)

80. *Pigmentation pattern consisting of generally small white spots on a black background.*

0: Absent.
1: Present.

A pigmentation pattern characterized by white spotting on a black background is present only in the Malagasy cichlid genus *Paratilapia*. (1.00)

81. *Triangular, black or dark gray pectoral-axil patch.*

0: Absent.
1: Present.

A black or dark gray pectoral-axil patch, which is visible dorsal to the pectoral-fin base in lateral view, is restricted to members of a clade comprising *Paretroplus damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe* (figs. 25A, 26, and 27). This patch is quite pronounced in *P. damii*. A similarly oriented and pigmented pectoral-axil patch is also present in *Ptychochromoides vondrozo* (fig. 21A) and *Etroplus canarensis*. (0.33, 0.60)

82. *Prominent black patch on pectoral fin near base.*

0: Absent.
1: Present.

A prominent black patch on the pectoral fin near its base is present only in the South Asian cichlid species *Etroplus suratensis* (figs. 21C and 25B) and *E. canarensis*. (1.00)

DISCUSSION

The morphological transformations (character descriptions presented in the Results section) supporting monophyly of Etroplinae, and various clades within this subfamily, are summarized and discussed below. Only unambiguous morphological transformations common to all most-parsimonious dichotomized trees are used to diagnose clades. Numbers in parentheses correspond to the characters listed above in Results. Unique and unreversed (= non-homoplasious) features are indicated by character number and appear in boldface type in the text. On the strict consensus topology (fig. 1), unique and unreversed (= non-homoplasious) features

are indicated on the branches by solid circles, whereas open circles designate homoplasious features. Character number appears above the branches, whereas the corresponding character state is listed below the branches.

Monophyly of Etroplinae (Clade A)

Etroplinae (sensu Sparks, 2004a; Sparks and Smith, 2004), comprising the endemic Malagasy genus *Paretroplus* and *Etroplus*, endemic to southern India and Sri Lanka, is monophyletic and supported by numerous morphological synapomorphies. The sister-group relationship between *Paretroplus* and *Etroplus* represents a well-corroborated, transoceanic sister-group pair. In the phylogenetic reconstruction based on the simultaneous analysis of anatomical features and nucleotide characters (fig. 1), Etroplinae is diagnosed by 31 unambiguously optimized morphological features, of which 28 are unique and unreversed (character number in boldface type): **(8)** the anterodorsal (= primordial) process of the anguloarticular is markedly elongate, curved, and tapered rostrally (fig. 3B); **(10)** the mesethmoid-maxillary ligament is robust and straplike; **(11)** the interopercular-mandibular ligament is continuous with the epihyal-interopercular ligament, such that there are not two distinct and well-separated (= discrete) ligaments; **(12)** the presence of a second premaxillary-maxillary ligament originating from the anterior portion of the articulating head of the maxilla (fig. 3B); **(13)** the median frontal canals and median frontal pores of the neurocranium are coalesced, forming a continuous median canal with a single dorsal pore (fig. 6C); **(14)** the exoccipital foramina are greatly enlarged, such that much of the lateral faces of these bones are lost, creating a dorsally projecting exoccipital chamber (figs. 7C and 8A–B); **(15)** the presence of a ventrocaudally directed supraoccipital-exoccipital prong, which extends ventrally over the foramen magnum (figs. 7C, 8B, and 10B); **(16)** excavation of the posterior margin of the supraoccipital bone, which becomes pronounced (wide and rounded) in members of Clade G (figs. 10B and 19C); **(17)** the foramen magnum is greatly enlarged (figs. 7C and 9B); **(18)** the frontal bones are bisected by the supraoccipital bone (figs. 6C and 10B); (19) the ethmovomerine region is extremely deep-bodied and beaked in lateral view (fig. 10B); **(20)** the presence of a ventral laminar extension to the median keel (= adductor process) of the parasphenoid (fig. 10B); (28) the presence of molariform teeth on the third pharyngobranchial tooth plates (fig. 11D); (29) the presence of molariform teeth on the fifth ceratobranchial tooth plates (fig. 14B); **(31)** the central ligament of the ventral branchial apparatus is bifurcate from its origin on the anterior margins of the fifth ceratobranchial bones; **(32)** the ventral flanges of the urohyal are narrow and horizontally oriented; **(34)** the median palatoprevomerine ligament inserts primarily on the entopterygoid and weakly on the ectopterygoid, but not at all on the palatine (fig. 15B); **(35)** the palatine is displaced dorsally, such that the ectopterygoid and entopterygoid are relatively more closely associated with the posterior margin of the prevomerine head; **(41)** the entopterygoid and metapterygoid are separated dorsally by a substantial gap, and the opposing margins of each bone bear strong interdigitations (fig. 15B); **(43)** the symplectic is complex and bears many spines along its ventrocaudal margin (fig. 15B); **(45)** the ventral margin of the cleithrum is broad, peglike, and flattened (fig. 17B); **(46)** well-developed, paired, and rostrally directed processes, which are widely separated from the vertebral centrum, are present on the anterior neural arches (figs. 10B and 18B, D); **(47)** the anterior neural arches are markedly widened (figs. 10B and 18B); **(48)** the anterior hemal spines bear anteroposteriorly oriented laminar extensions, which may connect or "interlock" (fig. 19C); **(49)** the anterior anal-fin pterygiophores insert into slots formed by laminar expansion of the anterior hemal spines (fig. 19C); **(50)** the anterior anal-fin pterygiophores are compressed and dorsocaudally directed (fig. 19C); **(51)** the anteriormost caudal vertebral centra bear accessory parapophyses; **(63)** the presence of broad caudal extensions of the gas bladder with corresponding compression of the anterior hemal spines and anal-fin pterygiophores (fig. 19C); **(67)** the presence of well-developed lateral ridges of scales (= scale sheath-

ing) along the bases of the dorsal and anal fins (fig. 22); **(69)** the presence of a well-developed pelvic axillary scale (fig. 23); and **(71)** the presence of a well-developed interpelvic scale series.

Monophyly of *Etroplus* (Clade B)

In the phylogenetic reconstruction based on the simultaneous analysis of anatomical features and nucleotide characters (fig. 1), the endemic southern Indian and Sri Lankan genus *Etroplus* Cuvier, in Cuvier and Valenciennes, 1830 is monophyletic and is recovered as the sister group to *Paretroplus*. *Etroplus* is diagnosed by three unambiguously optimized morphological features, all of which are unique and unreversed (character number in boldface type): **(4)** oral jaw dentition comprised of tricuspid teeth in both inner and outer rows (fig. 4C); **(36)** the presence of a single lacrimal plate (fig. 16E); and **(53)** an asymmetrical displacement of the first anal-fin pterygiophore to the left and the second to the right of the hemal spine complex (Stiassny et al., 2001: fig. 4). Rarely the reverse configuration occurs, in which the first anal-fin pterygiophore is displaced to the right and the second to the left of the hemal spine complex, although this condition is still unique to *Etroplus* (personal obs.). Although an anal-fin spine count of 10 or greater (generally 12–14), with several anterior pterygiophores associated with the first hemal spine, is unique to *Etroplus* (Character 56; state 2), this feature does not optimize unambiguously at this node (i.e., Character 56 is a multistate character in which state one is restricted to *Paretroplus*, the sister taxon to *Etroplus*).

Type Species: *Etroplus suratensis* (Bloch, 1790).

Included Species: *Etroplus maculatus* (Bloch, 1795); *Etroplus canarensis* Day, 1877.

Monophyly of *Etroplus suratensis* + *Etroplus canarensis* (Clade C)

Monophyly of Clade C, which comprises *Etroplus suratensis* and *E. canarensis*, is supported by the following three unambiguously optimized morphological features, one of which is unique and unreversed (indicated in boldface type): (65) the presence of a blunt snout with a steeply sloping profile in lateral view (particularly in specimens < about 75mm SL) (fig. 21C); (76) the presence of seven to nine prominent dark lateral bands (fig. 21C); and **(82)** the presence of a prominent black patch on the pectoral fin near its base (fig. 25B).

Monophyly of *Paretroplus* (Clade D)

In the phylogenetic reconstruction based on the simultaneous analysis of anatomical features and nucleotide characters (fig. 1), the endemic Malagasy genus *Paretroplus* Bleeker, 1868 is monophyletic and is recovered as the sister taxon to *Etroplus*. *Paretroplus* is diagnosed by 12 unambiguously optimized morphological features, nine of which are unique and unreversed (character number in boldface type): **(3)** the presence of spatulate, unicuspid dentition in a single row in both upper and lower jaws (figs. 3B, 4D, and 5A); (5) greatly enlarged and elongate teeth on either side of the premaxillary symphysis, with correspondingly small symphyseal teeth in the lower jaw (fig. 5A); **(6)** oral dentition is restricted anteriorly on the premaxillary arcade and dentary (figs. 3B and 4D); **(7)** there are very few teeth in both upper (18 or fewer) and lower (14 or fewer) oral jaws (figs. 3B and 4D); **(9)** the dorsal (= primordial) process of the anguloarticular is in close apposition to the posterior margin (= coronoid process) of the dentary (figs. 3B and 4D); **(23)** the first pharyngobranchial articulates with the parasphenoid only or at the parasphenoid-prootic margin; (33) the maxillary process of the palatine is elongate and tapered rostrally (fig. 15B); (37) the lacrimal is anteroventrally expanded, elongate, and paddle-shaped (fig. 16D); **(40)** along its anterodorsal margin the entopterygoid bears a flange or "calyx", which partially overlies the dorsomedial surface of the ectopterygoid and forms a slot into which the median palatoprevomerine ligament inserts (fig. 15B); **(44)** there is a substantial gap between the symplectic and the preopercle in lateral view, with no overlap between these two bones (fig. 15B); **(61)** the paired anterior

gas bladder bullae are complex and polyplike (= teardrop shaped), with extremely narrow connections to the main gas bladder chamber (figs. 18D and 20B-C); and **(62)** the anterior gas bladder bullae exhibit a tough, thickened, and rigid tunica externa (fig. 18D).

TYPE SPECIES: *Paretroplus damii* Bleeker, 1868. Type species by monotypy.

INCLUDED SPECIES: *Paretroplus damii* Bleeker, 1868; *Paretroplus polyactis* Bleeker, 1878; *Paretroplus petiti* Pellegrin, 1929; *Paretroplus kieneri* Arnoult, 1960; *Paretroplus maculatus* Kiener and Maugé, 1966; *Paretroplus menarambo* Allgayer, 1996; *Paretroplus nourissati* (Allgayer, 1998); *Paretroplus maromandia* Sparks and Reinthal, 1999; *Paretroplus tsimoly* Stiassny et al., 2001; *Paretroplus dambabe* Sparks, 2002a; *Paretroplus gymnopreopercularis*, new species; *Paretroplus lamenabe*, new species.

MONOPHYLY OF THE *PARETROPLUS DAMII* CLADE (CLADE E)

Monophyly of Clade E (= the *Paretroplus damii* clade), which comprises *P. damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, is supported by the following five unambiguously optimized morphological features, two of which are unique and unreversed (indicated in boldface type): **(70)** the posterior field of the lateral body scales is thin and not ossified (figs. 22B and 23C); (72) multiple discrete rows of scales extend onto both the soft dorsal and anal fins (fig. 22B); (73) the chest scales are markedly reduced in size and highly embedded (fig. 23C), with belly scales along the ventral midline exhibiting the greatest reduction in size; **(74)** multiple rows of scales that are markedly reduced in size extend laterally on the flanks dorsal to the pelvic fins and anus (fig. 23C); and (81) presence of a triangular, black or dark gray, pectoral-axil patch (fig. 25A).

MONOPHYLY OF THE *PARETROPLUS* "LAMENA" CLADE (CLADE F)

Monophyly of Clade F (= *Paretroplus* "lamena" clade), which comprises *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, is supported by two unambiguously optimized morphological features, one of which is unique and unreversed (indicated in boldface type): (21) the presence of elongate nasal bones; and **(77)** the presence of two wide and convergent, black midlateral bands on the flanks (figs. 23C and 24C).

MONOPHYLY OF CLADE G

Clade G comprises the *Paretroplus kieneri* species complex (Clade H) and a clade comprising the deep-bodied and disk shaped members of *Paretroplus* (Clade I). Monophyly of Clade G is supported by one unique and unreversed, unambiguously optimized morphological feature: **(16)** the presence of a large, wide, and rounded excavation (= incut) on the posterior margin of the supraoccipital bone (figs. 10B and 19C).

MONOPHYLY OF THE *PARETROPLUS KIENERI* COMPLEX (CLADE H)

Monophyly of Clade H (= the *Paretroplus kieneri* complex), which comprises *P. kieneri* and *P. gymnopreopercularis*, is supported by one unique and unreversed, unambiguously optimized morphological feature: **(79)** the presence of a blotchy orange, gray, and brown pigmentation pattern. Members of this clade are the only species of *Paretroplus* to completely lack any traces of a vertical banding pattern (fig. 24D).

MONOPHYLY OF THE DEEP-BODIED *PARETROPLUS* CLADE (CLADE I)

Monophyly of Clade I, comprising all of the deep-bodied and essentially disk-shaped members of *Paretroplus* (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, *P. petiti*, and *P. polyactis*) is supported by three unambiguously optimized morphological features, two of which are unique and unreversed (indicated in boldface type): **(66)** the presence of a deep and more or less disk-shaped body (figs. 19C, 21D, and 24A–B); **(68)** the presence of lateral ridges of scales ("scale sheathing") that are free from the fin membranes over the entire length of the soft dorsal and anal fins (fig. 22A); and (76) the presence of seven to nine prominent dark lateral bands (fig. 24A–B).

Monophyly of the Deep-Bodied Western *Paretroplus* Clade (Clade J)

Monophyly of Clade J, comprising the deep-bodied members of *Paretroplus* that are confined to western basins (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*) is supported by two unambiguously optimized morphological features, one of which is unique and unreversed (indicated in boldface type): (65) the presence of a blunt snout, with a steeply sloping profile in lateral view (figs. 21D and 24B); and **(75)** a distinctive horizontal striping pattern of alternating light and dark stripes extending from the anterior margin of the orbit to origin of the caudal fin (fig. 24B).

Gas Bladder Evolution in Malagasy–South Asian Cichlid Fishes

One of the most remarkable features of the Malagasy and South Asian cichlids, and in particular members of Etroplinae, is the development of the anterior of the gas bladder and corresponding changes to the posterior of the neurocranium to create a direct (= otophysic) connection between the gas bladder and inner ear (fig. 20). Apart from these lineages, in no other cichlids (e.g., the species-rich African and Neotropical assemblages) does the gas bladder contact, or even closely approach, the neurocranium. In contrast, the Malagasy–South Asian cichlids are characterized by extreme modifications of the anterior gas bladder in the form of paired anterior extensions and corresponding changes to the posterior and otic region of the neurocranium (fig. 20).

In recent studies, the Malagasy and South Asian cichlids either comprise a monophyletic assemblage that includes two major lineages, Etroplinae and Ptychochrominae (Sparks, 2001, 2004a), or Ptychochrominae has been recovered as the sister taxon to a monophyletic African-Neotropical clade (Sparks and Smith, 2004), such that Etroplinae is recovered as the sister taxon to a clade comprising Ptychochrominae plus the African and Neotropical lineages. In the study of Sparks and Smith (2004), the major cichlid clades are each robustly monophyletic (i.e., African, Neotropical, African + Neotropical, Etroplinae, and Ptychochrominae). Thus, the sister group to the highly specialized Etroplinae is either the moderately specialized Ptychochrominae, or Ptychochrominae plus a species-rich unspecialized lineage (African + Neotropical). The phylogenetic placement of Ptychochrominae is a problem that has plagued all family-level studies of cichlids to date.

The Malagasy and South Asian cichlids are characterized by the presence of enlarged exoccipital foramina (absent in other cichlids) (Stiassny, 1991), and most species exhibit paired anterior extensions of the gas bladder that either contact the exoccipital region of the neurocranium (strongly or via connective tissue as in *Ptychochromis* and *Ptychochromoides*; fig. 20A), or the gas bladder extends through the enlarged exoccipital foramina and expands into large intracranial bullae that are in direct contact with the labyrinth, thus forming a direct otophysic connection between the gas bladder and inner ear (*Etroplus* and *Paretroplus*; fig. 20B–C) (Dehadrai, 1959; Sparks, 2001; Stiassny et al., 2001). These unique anatomical features would seem to provide compelling evidence to suggest that the Malagasy–South Asian cichlids comprise a monophyletic assemblage (Stiassny, 1991; Sparks, 2001), despite initial contradictory evidence from nucleotide characters (Sparks and Smith, 2004: fig. 1).

Although anterior gas bladder extensions of some form are present in almost all cichlids, they seldom extend much anterior of the first pleural ribs (e.g., apart from the Malagasy–South Asian lineages, anterior gas bladder horns are most pronounced in the Neotropical genera *Chaetobranchopsis* and *Geophagus*, and the monotypic African genus *Heterochromis*). Nonetheless, paired anterior gas bladder chambers that approach or contact the exoccipital region of the neurocranium do not occur in any non-Malagasy–South Asian cichlid species. Of the Malagasy–South Asian lineages, only *Oxylapia* and *Katria* (fig. 10A) lack paired anterior gas bladder extensions that at least contact the exoccipital bones. In *Paratilapia* the anterior gas bladder horns are well developed, and although they always contact the exoccipital region of the neurocranium, in some speci-

mens I have observed that they actually penetrate the exoccipital foramina.

Members of Etroplinae exhibit the most highly modified and complex gas bladder–neurocranial morphologies of any cichlids (figs. 18D, and 20B–C). Gas bladder structure in members of Ptychochrominae ranges from more or less unspecialized to moderately specialized, in which the anterior gas bladder horns abut the exoccipital region of the skull (fig. 20A). In contrast, the paired anterior gas bladder extensions found in all members of Etroplinae are firmly lodged in and expanded within the characteristic exoccipital foramina (comprising both an inner and outer chamber), such that they form a direct mechanical (= otophysic) linkage between the gas bladder and inner ear. In *Paretroplus* these structures become the most highly modified, and the multiple anterior polyplike chambers (= bullae) exhibit a tough and thickened tunica externa, with extremely narrow connections (diverticula) to the main gas bladder chamber (and in some cases to each other) (fig. 20C).

In members of Etroplinae, a number of corresponding modifications of associated structures (e.g., large exoccipital foramina, excavation of the posterior margin of the supraoccipital crest [particularly pronounced in species of *Paretroplus* that inhabit lacustrine environments], the presence of a supraoccipital-exoccipital prong, enlargement and modifications of the foramen magnum, and enlarged and expanded anterior neural arches) have also been observed (Sparks, 2001; Stiassny et al., 2001; e.g., figs. 7C, 8A–B, 9B, 10B, 18D, and 20B–C). These associated structures appear to be encompassed by a "tent" of connective tissue that envelops the posterior margin of the skull (i.e., including portions of the supraoccipital, the supraoccipital-exoccipital prong, and surrounding the dorsal margins of the enlarged anterior neural arches and foramen magnum) (Sparks, 2001). It is hypothesized that these modifications contribute to increased hearing capacity or sound transmission. Indeed, the single species of *Paretroplus* examined to date (*P. menarambo*) is found to have enhanced hearing ability relative to other cichlids that have been tested, and, surprisingly, can hear about as well as the goldfish (C. Braun, unpubl. data). In addition, preliminary studies of *Paretroplus* using high resolution CT scans reveal that the tough-walled anterior gas bladder bullae that enter the neurocranium are closely apposed to the labyrinth (unpubl. data).

Within Cichlidae, and the Malagasy–South Asian lineages in particular, we have an excellent model system in which to study the origins, diversification, and function of hearing-related morphological transformations. Results of the comparative studies presented herein reveal a broad range of accessory hearing specializations and trends of increasing hearing-related specializations within the Malagasy and South Asian lineages, which range from unspecialized (e.g., *Oxylapia polli* and *Katria katria*) to multiple (potentially convergent) examples of complex and highly modified forms (e.g., *Paratilapia*, *Ptychochromoides*, *Ptychochromis*, and in particular, *Etroplus* and *Paretroplus*).

KEY TO THE GENERA OF MALAGASY AND SOUTH ASIAN CICHLIDS

1a. Anal-fin spines number seven or greater (fig. 19C); pelvic axillary scale present (fig. 23); scale ridges ("sheathing") present on dorsal and anal fins near base and free from fin membrane on spiny portions of both fins (fig. 22); scales cycloid 2

1b. Anal-fin spines number three (or rarely four) (fig. 19A–B); absence of pelvic axillary scale (fig. 21A–B); absence of scale ridges ("sheathing") along dorsal- and anal-fin bases (fig. 21A–B); scales mostly ctenoid (except *Paratilapia*, which is variable for this feature) 3

2a. Oral dentition unicuspid, spatulate in shape; a single row of teeth in both upper and lower jaws; teeth few in number (≤ 18 in upper jaw, ≤ 14 in lower); upper-jaw teeth on either side of premaxillary symphysis greatly enlarged (figs. 3B, 4D, and 5A) . . . . . *Paretroplus*

2b. Oral dentition tricuspid (both inner and outer rows); teeth present in multiple rows in both upper and lower jaws; teeth numerous (in much greater numbers than *Paretroplus*) on both upper and lower jaws (fig. 4C) . . . . *Etroplus*

3a. Oral dentition comprised entirely of caniniform (conical) teeth in both upper and lower jaws (figs. 3A and 5B); teeth numerous; fourth ceratobranchial tooth plates absent;

generally jet black in coloration with smallish white spotting . . . . . *Paratilapia*

3b. Caniniform (conical) teeth absent; oral dentition either bicuspid and bilaterally symmetrical, robust and unicuspid, or a combination of both morphologies (fig. 4B); fourth ceratobranchial tooth plates present (fig. 12B) . . 4

4a. Oral dentition comprised of wide, generally unicuspid teeth that are expanded and flattened at the crown; otherwise, teeth may be weakly to moderately bicuspid; inner row teeth always unicuspid; teeth few in both upper and lower jaws; first anal-fin spine not greatly reduced in length; pelvic spine hypertrophied; pelvic fins robust; dark vertical bar present under orbit . . . . . *Oxylapia*

4b. Oral dentition comprised of bilaterally symmetrical, bicuspid teeth; both inner and outer rows of the same morphology (fig. 4B); teeth numerous in both upper and lower jaws; first anal-fin spine greatly reduced in length (fig. 19B); pelvic spine not hypertrophied; vertical suborbital bar lacking (fig. 21) . . 5

5a. Presence of a free tooth plate associated with, but not fused to, the second epibranchial bone (fig. 11A–B); third infraorbital bone excluded from orbit margin by second infraorbital; 26 to 28 vertebrae (fig. 19B) . . . . . *Ptychochromis*

5b. Absence of a free tooth plate associated with the second epibranchial bone (fig. 11C); third infraorbital bone included in orbit margin (fig. 16C); 29 to 31 vertebrae (rarely 28) . . 6

6a. A single row of teeth present on the second pharyngobranchial tooth plate (fig. 11C); blotchy and mottled grayish-black or brownish overall coloration (fig. 21A); 10 to 13 gill rakers present on the lower limb of the first arch . . . . . *Ptychochromoides*

6b. Two rows of teeth present on the second pharyngobranchial tooth plate; overall coloration and pigmentation pattern consisting of two prominent black vertical bars on an iridescent golden background; eight or nine gill rakers present on the lower limb of the first arch . . . . . *Katria*

KEY TO THE SPECIES OF *PARETROPLUS*

1a. Posterior field of (lateral) scales thin, "flap-like", and not ossified (figs. 22B and 23C); small black patch present immediately above pectoral-fin origin (fig. 25A); multiple discrete rows of scales extend onto both the soft dorsal and anal fins (fig. 22B); chest scales markedly reduced in size and highly embedded (fig. 23C); multiple rows of scales, markedly reduced in size, extend dorsal to the pelvic fins from the chest to the anus (fig. 23C) 2

1b. Posterior field of (lateral) scales ossified, not "flap-like" (figs. 22A and 23A–B); black patch absent immediately above pectoral-fin origin (figs. 23A–B and 24A–B); scales not extending onto soft dorsal or anal fins (fig. 22A); chest scales not reduced to at most slightly reduced in size (fig. 23A–B) 5

2a. Dorsal-fin spines 14–17; anal-fin spines 7–8 (rarely 9); presence of two wide, prominent, and convergent dark brown to black midlateral bands (figs. 24C and 45); additional bands present, but more subtle, except posteriorly in *P. tsimoly* (figs. 51, 52)] . . . 3

2b. Dorsal-fin spines 18–20; anal-fin spines 9–11; no prominent vertical barring on flanks (figs. 26, 27); coloration solid gray to grayish brown (when sexually quiescent) . . *P. damii*

3a. Body depth 47.0%–54.3% SL; pelvic fins extend beyond origin of anal fin when adducted (figs. 58, 59) . . . . . *P. lamenabe*

3b. Body depth 38.15%–46.8% SL; pelvic fins not extending beyond origin of anal fin when adducted (figs. 45, 46 and 51, 52) 4

4a. Lips enlarged and lobed; lips bluish (in life) to bluish-gray (in preservation) in adults; posteriormost four or five bars on flank, including centralmost two bars, about equally pigmented (figs. 51, 52) . . . . . *P. tsimoly*

4b. Lips not enlarged or lobed regardless of size; base coloration in sexually active individuals bright red in life; centralmost two bars on flank the most heavily pigmented in adults (figs. 45, 46) . . . . . *P. nourissati*

5a. Gill rakers on lower limb of first arch (excluding raker in the angle of the arch) number 11 to 13 (mode 12); seven to nine prominent dark charcoal or black, broad vertical bars on flanks; scale margins dark and lending a chain-link or grated appearance to species; iris of eye red in life; only barred member of genus found in eastern drainages of Madagascar (figs. 24A and 30–32) . . . . . *P. polyactis*

5b. Gill rakers on lower limb of first gill arch (excluding raker in the angle of the arch) number 8 to 10 (rarely 11 and only in *P. maculatus*); prominent, darkly pigmented vertical bars absent in adults (except *P. maromandia*), although faint broad vertical bars may be present (e.g., figs. 24B, 34, 39, 40, 42, 43, and 53); all restricted to northwestern Madagascar 6

6a. Blotchy and mottled overall pigmentation pattern; absence of any trace of vertical barring pattern on flanks (figs. 24D, 36, 37,

Fig. 26. *Paretroplus damii*, syntype, RMNH 3939, 69.2 mm SL; northwestern Madagascar: Antsiranana Province: island of Nosy Be: Lake Pambilao.

and 55, 56); body depth not exceeding 56% of standard length (usually less than 50% of SL); anal-fin rays 11–13 7

6b. Presence of alternating light and dark horizontal striping pattern on flanks (fig. 24B); vertical barring on flanks present yet always faint in adults, and becoming nearly indistinguishable in large adults (fig. 21D; except *P. maromandia* [figs. 49, 50]); body depth exceeding 57% of standard length in adults; anal-fin rays 13 to 16. 8

7a. Preopercle fully scaled or scaled except along ventral margin (fig. 57A); predorsal profile mostly straight and snout pointed; generally

Fig. 27. *Paretroplus damii*, AMNH 232457, adult, 138.0 mm SL, from northeastern, Mahanara River, population (known locally as "ventitry").

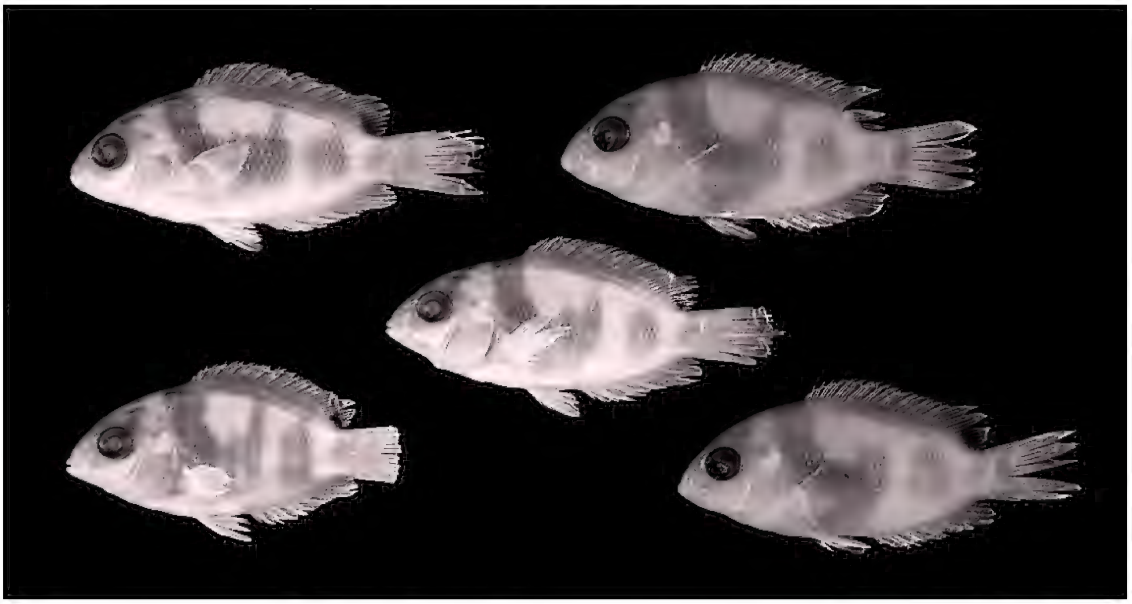


Fig. 28. Juvenile pigmentation pattern in *Paretroplus damii*, UMMZ 235023, 21.7–24.5 mm SL; Mananjeba drainage basin: Andranomaloto River. Mottled juvenile pigmentation pattern is lost by about 30–40 mm SL.

dark gray in coloration, particularly on head and fins (figs. 36, 37) . . . . . *P. kieneri*

7b. Preopercle asquamate (fig. 57B); snout blunt and predorsal profile strongly convex; orangish brown, golden brown, or yellowish in overall coloration (never dark gray) (figs. 55, 56) . . . . . *P. gymnopreopercularis*

8a. Vertical barring on flanks prominent; only member of *Paretroplus* with light base coloration and prominent, contrasting, dark bars on flanks as adults (figs. 49, 50); vivid red pigmentation below lateral midline on flanks in life . . . . . *P. maromandia*

8b. Vertical barring pattern on flanks always faint, regardless of size (e.g., figs. 21D, 24B, 34, and 53) 9

9a. Large, prominent rounded black patch present anteriorly on flanks, posterior of pectoral-fin insertion, and below upper branch of lateral line (figs. 24B and 39, 40) *P. maculatus*

9b. Black patch on anterior flank absent (e.g., figs. 21D, 34, and 53) 10

10a. Overall base coloration light; pale yellowish to olive; only light colored member of *Paretroplus* with faint barring pattern on flanks (figs. 53, 54); vivid red pigmentation (primarily on lower flanks) in life . . . . . *P. dambabe*

10b. Overall base coloration dark brown or dark grayish brown with no additional distinguishing marks, apart from obvious pattern of alternating horizontal light and dark stripes on flanks and weak vertical barring pattern (figs. 21D, 34, 42, 43) 11

11a. Scales in lateral line number 39; dorsal-fin rays 18; anal-fin rays 14 (fig. 34) . . *P. petiti*
Note: Counting last split ray, if split completely to fin base, as two elements.

11b. Scales in lateral line number 34 to 38 (mode 37); dorsal-fin rays 19–21; anal-fin rays 15–17 (figs. 21D, 42, 43) . . . . . *P. menarambo*
Note: Counting last split ray, if split completely to fin base, as two elements.

SPECIES ACCOUNTS

Paretroplus damii Bleeker, 1868
Figures 26–29; plate 1A; table 2

Paretroplus vandami: Sauvage, 1891: pl. 46 (misnamed in caption; see footnote p. 446).

Paretroplus dami: Boulenger, 1899: 142 (does not mention or justify spelling change for species name).

Paretroplus dami: Pellegrin, 1904: 322; Pellegrin, 1933: 115; Kiener and Maugé, 1966; Stiassny et al., 2001; Sparks, 2002a: table 1; Sparks, 2004a: fig. 3.

Paretroplus nov. sp. "dridrimena": Sparks and Stiassny, 2003: table 9.1.

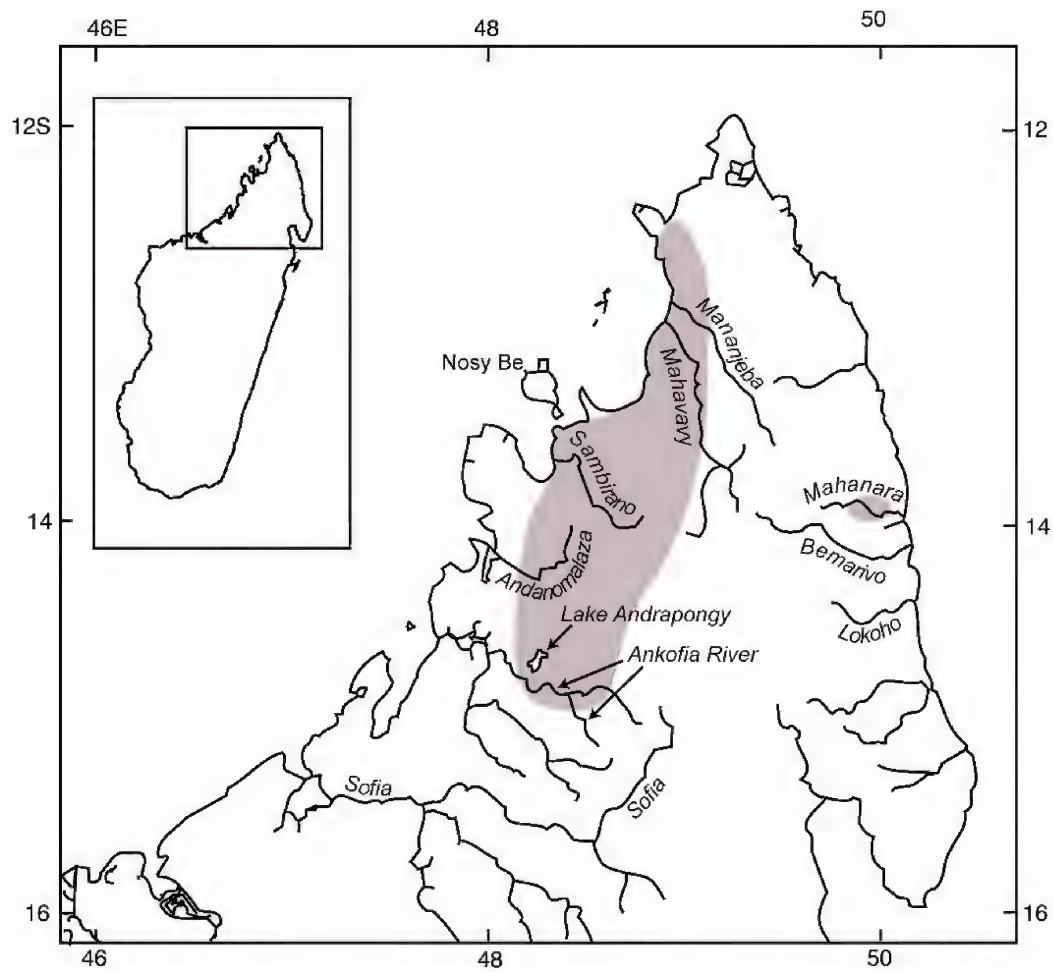


Fig. 29. Drainage map of northern Madagascar illustrating geographic range for *Paretroplus damii*, the only species of *Paretroplus* that occurs in both eastern and western drainages. These distributions should be regarded as approximations, as many remote northern drainage basins remain poorly surveyed (see Sparks and Stiassny, 2003; Sparks, 2004).

Paretroplus nov. sp. "ventitry": Sparks and Stiassny, 2003: table 9.1.

Paretroplus sp. Mahanara River: de Rham and Nourissat, 2004: 117–118.

SYNTYPES: RMNH 3939, 1 ex., 69.2 mm SL; northwestern Madagascar: island of Nosy Be: Lake Pambilao ["Nossibe (Lacus Pambilao)"]; Van Dam and F. Pollen. RMNH 4478, 1 ex., 58.2 mm SL; northwestern Madagascar: island of Nosy Be: Lake Pambilao; Van Dam and F. Pollen.

NOTES ON TYPE LOCALITY: Bleeker (1868: 311–314) originally described this species based on two specimens from "Nossibe (Lacus Pambilao)", which most certainly refers to Lac Ampombilava on the satellite island of Nosy Be, located off of the northwest coast of Madagascar. This type locality has been questioned, given that no specimens referable to *P. damii*, other than those described by Bleeker in the type series, have subsequently been collected from the island of Nosy Be, despite substantial effort. De Rham and Nourissat (2004: 113–114) report that their Malagasy guide recently collected specimens of *P. damii* from Lake Djabala (an adjacent crater lake to the presumed type locality) on the island of Nosy

TABLE 2

Morphometric and meristic data for *Paretroplus damii*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (S1) indicates counts corresponding to syntype RMNH 4478 and (S2) to syntype RMNH 3939. Note: In this and all subsequent data tables type material (if present) is included in number of specimens examined, and in range, mean, and standard deviation calculations.

		P. damii				
		Syntypes				
Character	N	4478	3939	Range	Mean	SD
Standard length (mm)	25	58.2	69.2	27.6–179.8	104.7	
Percentage of SL						
Head width (max.)	25	15.8	16.5	15.8–20.2	17.8	1.00
Head length	25	33.5	32.7	30.5–34.5	32.5	1.09
Body depth	25	49.3	47.8	45.3–55.9	50.2	2.66
Caudal peduncle length	25	4.6	6.4	4.6–7.3	5.8	0.79
Caudal peduncle width	25	2.8	3.5	2.3–5.0	3.8	0.70
Caudal peduncle depth	25	14.1	15.0	13.0–17.0	15.5	0.89
Pectoral-fin length	25	25.3	24.9	20.1–25.3	23.2	1.23
Pelvic-fin length	25	23.9	23.6	20.2–25.4	22.5	1.29
Pre-dorsal length	20	43.8	45.4	43.3–50.0	45.9	1.51
Pre-anal length	20	62.7	57.1	57.1–64.3	60.8	1.90
Pre-pelvic length	20	45.4	40.9	38.8–46.2	41.8	2.34
Percentage of HL						
Snout length	25	40.0	41.6	31.6–56.1	46.6	6.03
Orbit diameter	25	34.9	33.6	21.6–40.0	29.1	4.55
Upper jaw length	25	26.2	25.2	25.2–33.2	29.0	1.97
Lower jaw length	25	26.7	31.4	26.7–36.9	34.8	2.21
Interorbital width	24	28.2	30.1	24.8–38.5	33.1	3.44
Preorbital depth	23	28.2	24.8	16.8–39.5	30.5	5.34
Caudal peduncle length/width	25	1.7	1.8	0.9–2.5	1.6	0.42
Caudal peduncle length/depth	25	0.3	0.4	0.3–0.6	0.4	0.06
Scales in lateral line	25	35 (1), 36 (1), 37 (11) (S1, S2), 38 (8), 39 (4)				
Scales: lateral line to dorsal fin	20	6 (10) (S1), 7 (9) (S2), 8 (1)				
Gill rakers (lower limb 1st arch)	25	11 (9), 12 (9), 13 (7) (S1, S2)				
Vertebrae (precaudal + caudal)	28	14 + 17 = 31 (4), 15 + 16 = 31 (10) (S1), 15 + 17 = 32 (14) (S2)				
Dorsal fin	28	XVIII 13 (1), XVIII 14 (2), XVIII 15 (2) (S1), XVIII 16 (1), XIX 13 (5) (S2), XIX 14 (6), XIX 15 (1), XX 11 (1), XX 12 (5), XX 13 (3), XX 14 (1)				
Anal fin	28	IX 11 (5), IX 12 (3) (S1,2), X 10 (6), X 11 (12), X 12 (1), XI 9 (1)				

Be, but neglected to preserve any material, concluding they were similar to specimens collected on the mainland.

NOTES ON TYPE SERIES: Although Eschmeyer (2006) lists two syntypes of *Paretroplus damii* under RMNH 3939, I was able to locate only a single specimen (69.2 mm SL) corresponding to this catalog number in the RMNH collections. The second syntype described by Bleeker (1868) is most likely a specimen cataloged under RMNH 4478 (the included label states "type" under the species name of "*Paretroplus dami*"). Eschmeyer (2006), however, includes this individual within the syntypic series of *Paretroplus polyactis* (Bleeker, 1878), a taxon for which he lists two syntypes. An examination of this specimen, a juvenile, shows it to be clearly referable to *P. damii*, not *P. polyactis* (cf. tables 2 and 3). The handwritten labels included with both specimens are in identical handwriting, both stating "type" under the species name of "*Paretroplus dami*" (misspelling probably following Boulenger, 1899). Both specimens also agree in total length with that reported by Bleeker (1868) in the original description of the species (80"' and 95"'), assuming that Bleeker reported total

lengths (TL). RMNH 3939 measures 90.5 mm TL (caudal slightly damaged distally) and RMNH 4478 measures 76 mm TL (caudal also slightly damaged distally). In addition, fin spine/ray counts and lateral scale counts for both specimens also correspond well to those reported by Bleeker. It is unclear why Eschmeyer (2006) lists RMNH 4478 as a syntype of *Paretroplus polyactis*. The two specimens described as *P. polyactis* by Bleeker (1878) are reported as measuring 67''' and 89''' (presumably also referring to TL), neither measurement of which corresponds to that of RMNH 4478 (76 mm TL; 58.2 mm SL). The specimen catalogued under RMNH 4478 and measuring 58.2 mm SL is herein considered to be a syntype of *P. damii*.

Additional Material Examined: AMNH 231248, 3 ex., 1 ex. C&S, 71.6–139.0 mm SL; Madagascar: Antsiranana Province: Mahanara River: main channel of Mahanara River at Antsirabe Nord, at bridge on Route N-5: 13°38′29.4″S, 49°57′48.6″E; P. V. Loiselle, 9-X-2000. AMNH 231257, 4 ex., 1 ex. C&S, 74.9–88.5 mm SL; Madagascar: Antsiranana Province: Mahanara River: main channel at Antsirabe-Nord, at bridge on route N-5: 13°58′29.4″S, 49°57′48.6″E; P. V. Loiselle, 13-X-2000. AMNH 232428, 2 ex., 48.0–49.0 mm SL; Madagascar: Antsiranana Province: Ifasy River at Ambodipont, Andraniaomby: adjacent oxbow lake: 13°22′7.8″S, 48°52′22.8″E; P. V. Loiselle, 25-X-2001. AMNH 232438, 3 ex., 77–108 mm SL; Madagascar: Antsiranana Province: Sambirano River at Ambodidimaka village: 13°45′18.0″S, 48°29′30.0″E; P. V. Loiselle and villagers, 26-X-2001. AMNH 232445, 3 ex., 20.0–25.0 mm SL; Madagascar: Antsiranana Province: Ramena River below bridge of Ambanja-Bemanevika road: 13°45′16.2″S, 48°31′9.6″E; P. V. Loiselle, J. Miandriaza, and local fishermen, 26-X-2001. AMNH 232457, 4 ex., 129.5–149.0 mm SL; Madagascar: Antsiranana Province: Mahanara River: ca. 4 km northwest of Antsirabe-Nord: 13°57′18.0″S, 49°56′12.0″E; P. V. Loiselle and local fishermen, 31-X-2001. AMNH 232461, 3 ex., 96.0–134.1 mm SL; Madagascar: Antsiranana Province: Mahanara River: at Antsirabe-Nord just upstream of bridge over route N-5: 13°58′29.4″S, 49°57′48.6″E; P. V. Loiselle and local fishermen, 1-XI-2001. AMNH 232473, 2 ex., 41.5–84.0 mm SL; Madagascar: Antsiranana Province: Ramena River at Antseva village: 13°42′42.4″S, 48°34′9.4″E; local fisherman and C. J. Raxworthy, 1-IV-2001. AMNH 236145, 112.5 mm SL; Madagascar: Antsiranana Province: Mahanara River, main channel at Antsirabe-Nord; P. V. Loiselle. AMNH 236154, 2 ex., 52.4–110.8 mm SL; Madagascar: Mahajanga Province: Anjingo River: main channel below bridge on Antsohihy-Bealanala Road; P. V. Loiselle, 2004. MHNG 2537.44, 7 ex., 91.4–162.2 mm SL; Madagascar: Mahajanga Province: Riviere Ankofia (= Anjingo) or Lac Andrapongy, environment Antsohihy: P. de Rham and J.-C. Nourissat, 17–19-X-1992. MHNG 2537.45, 6 ex., 98.6–154.3 mm SL; Madagascar: Mahajanga Province: Lac Andrapongy, environment Antsohihy: P. de Rham and J.-C. Nourissat, 17-X-1992. MHNG 2640.040, 1 ex., 141.0 mm SL; northern Madagascar: Ansiranana Province (Diego Suarez): Ramena River, near mouth of Sambirano River; P. de Rham and J.-C. Nourissat, X-1999. MNHN 1931-0225, 1 ex., 69.0 mm SL; Antsiranana Province: Sambirano: Coll. by Waterlot. UMMZ 233523, 14 ex., 6 ex. S, 123–179 mm SL; northwestern Madagascar: Mahajanga Province: probably Anjingo River. UMMZ 235021, 37 ex., 1 ex. C&S, 31–138 mm SL; northwestern Madagascar: Mahajanga Province: east of Antsohihy: Anjingo River (upstream and downstream of bridge over RN31): 14°50′41.0″S, 48°14′38.0″E; JSS94-19; J. Sparks and K. Riseng, 28-VII-1994. UMMZ 235022, 34 ex., 1 ex. C&S, 82–170 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Lac Andrapongy, north basin: 14°41′49.0″S, 48°07′54.0″E; JSS94-21B; J. Sparks and K. Riseng, 1994. UMMZ 235023, 51 ex., 3 ex. C&S, 9–182 mm SL; northwestern Madagascar: Antsiranana Province: north of Ambanja: Andranomaloto River (tributary of Mananjeba River): 13°12′46.0″S, 49°10′34.0″E; JSS96-22; J. Sparks and K. Riseng, 15-VII-1996. UMMZ 239543, 5 ex., 1 ex. C&S, 56–72 mm SL; northwestern Madagascar: Mahajanga Province: northeast of Antsohihy: Anjingo River at RN31:

14°50′39.0″S, 48°1′39.0″E; JSS94-54; J. Sparks and K. Riseng, 15-XI-1994. UMMZ 239544, 5 ex., 73–158 mm SL; northwestern Madagascar: Antsiranana Province: market purchase near Ambanja: J. Sparks and K. Riseng, VII-1996. UMMZ 240355, 1 ex., S, 86 mm SL; no locality data, aquarium specimen.

DIAGNOSIS: A *Paretroplus* belonging to Clade E, comprising *P. damii*, *P. nourissati*, *P. tsimoly*, and *P. lamenabe*, and distinguished from all congeners by the presence of a triangular, black pectoral-axil patch in combination with the absence of a series of vertical bars on the flanks. In life, unstressed individuals can easily be distinguished from all congeners by the presence of a broad, vertical pale yellow band on the anterior half of the flanks. Young *P. damii* are unique among congeners in the possession of a dark blotch, surrounded by a hyaline ring, posteriorly on the soft dorsal fin near its base. In preservation, *P damii* is the only member of *Paretroplus* that exhibits a solid grayish-brown to brown base coloration and the absence of vertical barring.

DESCRIPTION: Morphometric and meristic data presented in table 2. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figures 26–28. A relatively shallow bodied *Paretroplus* belonging to Clade E: fig. 1), which also includes *P. nourissati*, *P. tsimoly*, and *P. lamenabe*. *Paretroplus damii* is the largest and most deep-bodied member of this clade, and specimens of nearly 40 cm TL have been collected (de Rham and Nourissat, 2004). Head moderately pointed, snout straight to slightly curved, and predorsal profile moderately curved. Dorsal body outline slightly curved, ventral outline mostly straight (except posteriorly). Caudal peduncle short, deep, and laterally compressed. No sexually dimorphic features apparent.

Total vertebral count 31 or 32, with formulae of: 14 + 17, 15 + 16, and 15 + 17, precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, other teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw number four to seven on each side, and total 12–13 (a single specimen was examined from UMMZ 235023 [C&S] with a total of eight teeth in the upper jaw). Teeth in lower jaw number five to seven on each side, and total 11–13. Teeth in both upper and lower jaws frequently irregularly spaced and graded in size laterally.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present, but only posteromedially on LPJ. LPJ well sutured, with numerous interdigitating sutures on posteroventral margin. Seven to nine robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Fourth ceratobranchial tooth plates not confluent with outer-row gill rakers of these elements. Individual tooth plates separate at base in smaller individuals, and becoming fused in larger specimens. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition) (fig. 13). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three rows.

Eleven to 13 triangular, somewhat elongate, gill rakers arrayed along lower limb of first gill arch. Rakers edentate in small individuals, becoming weakly denticulate dorsomedially in larger specimens. All other lower-limb rakers (i.e., gill arches 2 through 4) short, triangular in shape (not spherical), and strongly denticulate dorsally. Epibranchial rakers on first gill arch elongate, numbering 9–11.

Body covered with large, regularly imbricate, cycloid scales. Posterior field (= caudal

margin) of flank scales thin, lacking circuli, and unossified, forming a flexible "flap". Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from spiny dorsal and anal fins, but becoming weakly attached to both soft dorsal and anal fins. Pelvic axillary scale present and well developed. Lateral-line scales number 35–39 (mode 37). Chest scales markedly reduced in size and embedded. Scales along ventral midline smallest. Four to five rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Snout, lacrimal, and anterior portion of interorbital region asquamate. Preopercle asquamate ventrally and only scaled on dorsal portion of shaft. Scales on caudal fin reduced in size and extending posteriorly about 1/2 to 2/3 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XVIII–XX spines, 11–16 soft rays. Anal with IX–XI spines, 9–12 soft rays. Origin of dorsal fin at about level of vertical through pectoral-fin insertion. Caudal fin weakly emarginate, and upper and lower lobes broad and more-or-less rounded. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins at most weakly produced and pointed in larger specimens. Pelvic fin extending to about level of anal-fin origin.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital foramina present (figs. 7C, 8A, and 9B). Paired anterior gas bladder bullae with tough and thickened tunica externa, anteriormost chambers firmly lodged in exoccipital recesses. Characteristic excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital either poorly developed or lacking (i.e., notch may be lacking entirely or, if present, ranges from shallow, narrow, and poorly developed in riverine populations to moderately pronounced in deeper-bodied, lacustrine populations). Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

Coloration in Life: Base body coloration ranges from golden brown, to grayish, to dark brownish olive (de Rham and Nourissat, 2004: 114–117). Triangular black patch present in the pectoral-fin axil, and visible in lateral view dorsal to pectoral-fin base. Fin coloration ranges from gray, to grayish brown, to dark brownish olive. Juveniles less than about 40 mm SL mottled (appear camouflaged) with characteristic large dark predorsal saddle and concentrated black blotch on posterior margin of soft dorsal fin (fig. 28). Unstressed individuals are dark gray to grayish brown and exhibit a wide, pale yellow band on the anterior flank. The head, dorsal opercle, cheek, interorbital region, and snout are also pale yellow in unstressed specimens. This pale yellow coloration quickly disappears if the fish is disturbed (see de Rham and Nourissat [2004: 116] for a photograph). In breeding individuals from west coast populations, this yellow region becomes brick red (P. Loiselle, personal commun.).

Coloration in Preservative: Large adults dark grayish brown to dark brown, and smaller specimens golden brown to gray; body somewhat darker dorsally, particularly in smaller individuals (fig. 27). Prominent triangular black patch present in pectoral-fin axil and extending dorsal to pectoral-fin base (fig. 25A). Wide, pale (yellowish) lateral band present in some large adults. Juveniles less than about 40 mm SL mottled gray, grayish brown, or golden brown, with concentrated black blotch present on posterior margin of soft dorsal fin (fig. 28).

Distribution and Habitats: Widespread in northwestern and far northern Madagascar (fig. 29). Along the northwestern versant of the island, the known range of *P. damii* extends in the south from the Anjingo-Ankofia River basin and Lake Andrapongy northward to the rivers (Sahinana and Sampiana) draining the western slopes of the Montagne d'Ambre massif in far northern Madagascar (de Rham and Nourissat, 2004). The species has also recently been collected by Paul Loiselle (NY Aquarium/WCS) from the middle reaches of the eastward draining Mahanara River to the

north of Sambava in northeastern Madagascar (fig. 29, gray circle). The geographic range of *P. damii* is noteworthy in that it is the only member of the genus that occurs in both eastward and westward draining basins.

LOCAL NAMES: *Damba*, *damba mena*, *lamena*, *dridrimena*, *ventitry*. De Rham and Nourissat (2004) also list *filaopisaka* and *loakapisaka* as local common names.

ETYMOLOGY: Named in honor of the Dutch naturalist Van Dam, who along with F. Pollen, collected the type material.

RELATIONSHIPS AND DISCUSSION: *Paretroplus damii* is the sister taxon to a clade (Clade F) comprising *P. tsimoly*, *P. nourissati*, and *P. lamenabe* (fig. 1). Clade F is diagnosed by the presence of two prominent and converging midlateral bands (several fainter bands are also present on the flanks) and elongate nasal bones, features that are both absent in *P. damii* (cf. figs. 24C and 25–27). Clade E, comprising *P. damii*, *P. tsimoly*, *P. nourissati*, and *P. lamenabe*, is united by five unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1).

It has been suggested that specimens historically assigned to *P. damii*, as well as populations of morphologically similar fishes recently discovered in far northern and northeastern Madagascar, represent more than one valid species, and possibly as many as three (P. Loiselle, personal commun.). These allegedly unique species have been referred to as *Paretroplus* sp. "dridrimena" (far northern Madagascar) and *P.* sp. "ventitry" (Mahanara drainage, northeastern Madagascar) (de Rham and Nourissat, 2002, 2004). *Paretroplus* sp. "dridrimena" is reported from the western slope of the Massif d'Ambre, and the Mananjeba, Mahavavy du Nord, and Ifasy rivers, all western drainages in northwestern Madagascar. *Paretroplus* sp. "ventitry" has to date been collected only in the Mahanara River drainage in northeastern Madagascar, north of the Masoala Peninsula.

The type locality for *P. damii* is a crater lake (Lake Ampombilava; recorded by Bleeker, 1868, as "Nossibe (Lacus Pambilao)") located on the island of Nosy Be, which lies only a few kilometers offshore from mainland Madagascar between the outlets of the Sambirano and Mananjeba rivers and their mainland tributaries (comprising a portion of the putative range of *P.* sp. "*dridrimena*", which extends northward to rivers draining the western slopes of Montagne d'Ambre) along the northwestern coast of Madagascar. During the course of this study, specimens from populations that represent both *P.* sp. "dridrimena" and *P.* sp. "ventitry" have been examined. Numerous lots of *P. damii* were also examined from throughout its range. No apomorphic features were identified to differentiate these allegedly distinct northern populations from *P. damii*. Given the close proximity to the type locality of *P. damii* and lack of apomorphic diagnostic features, specimens that have been referred to *P.* sp. "dridrimena" are instead concluded to be conspecific with *P. damii*. Likewise, the Mahanara River population, *P.* sp. "ventitry", located on the northeastern coast and opposite to the Mananjeba River and its tributaries on the western coast, appears to be indistinguishable from *P. damii* on the basis of apomorphic morphological features. Therefore, it is concluded herein that the populations from northern Madagascar that have been referred to as "ventitry" and "dridrimena" do not warrant recognition as distinct species.

This statement should not be taken to indicate that additional study is not likely to reveal features useful for distinguishing among these geographic populations, and in particular between the single known east-coast ("ventitry") and various western populations (including "dridrimena"). For example, despite some overlap in all of the following characteristics, in overall appearance, members of the east-coast "ventitry" population are in general more shallow bodied, the caudal peduncle is usually more elongate, and they are generally more darkly pigmented as adults than *P. damii* confined to western basins. In addition, the east-coast "ventitry" population differs in breeding coloration from all known west-coast populations of *P. damii*. Sexually active "ventitry" individuals are bright golden yellow and black, versus brick red and black in western populations of *P. damii*.

Nucleotide characters may prove useful in differentiating the various populations currently included in *P. damii*; however, preliminary results to date indicate that nucleotide sequence divergence among these populations is quite low (W. L. Smith and J. S. Sparks, unpubl. data). In addition, based on DNA sequence data collected to date for other species shared between the mainland (i.e., occurring in the Mananjeba River and its tributaries) and Nosy Be (e.g., *Ptychochromis oligacanthus* and *Paratilapia polleni* [Sparks, 2003; Stiassny and Sparks, 2006]), landmasses which have repeatedly been connected during periods of low sea level resulting from Recent and Pleistocene glaciations, differences between mainland and Nosy Be populations of *P. damii*, should the latter be extant (e.g., see Loiselle, 2005), are anticipated to be minimal.

Paretroplus polyactis Bleeker, 1878
Figures 30–33; plate 1B; table 3

Chromis madagascariensis: Guichenot, 1866: *nomen nudum*. Pellegrin, 1904: 323 (359), listed as *nomen nudum* under synonymies for *Paretroplus polyactis*.

Paretroplus damii (*non* Bleeker, 1868): Steindachner, 1880: 247. Pellegrin, 1904: 323, in synonymy with *Paretroplus polyactis*.

NOTES ON SYNTYPES AND TYPE LOCALITY: Bleeker (1878) included two specimens (67 and 89 mm [presumably] TL) in his original description of *P. polyactis*. No catalog numbers for these syntypes accompany the description, which is consistent for that time period. Bleeker (1878: 196) reported that the type specimens were collected from rivers in eastern Madagascar near the town of "Manahare" ("Madagascar orientalis (Manahare); in fluviis"); however, I am unable to locate any town with that exact spelling in eastern coastal Madagascar. It has generally been assumed that Bleeker was referring to the large town of Mananara (P. Loiselle, personal commun.), located near the mouth of Antongil Bay in the northeast (and between Maroansetra and Toamasina), and that "Manahare" was simply a phonetic misspelling. The type series was collected by J.-P. Audebert, a German naturalist who collected along Madagascar's eastern coast from 1876 to 1880, and who presumably spent 1876 collecting in northeastern coastal localities from Antongil Bay southward to Toamasina (Tamatave) (Carleton and Schmidt, 1990: 18). As Carleton and Schmidt (1990) point out, "Audebert's orthographic renditions of Malagasy place names, however, have challenged attempts to associate them with conventional geographic spellings and created considerable uncertainly about the distribution of the taxa he collected". Carleton and Schmidt (1990) indicate "Mananare" is probably simply a phonetic misspelling of Mananara (as many other localities reported by Audebert contain similar phonetic misspellings). It is not a stretch to assume that Bleeker (1878) added to the confusion with his phonetic interpretation ("Manahare"). Nevertheless, in a detailed journal of his travels in northern Madagascar, the Rev. Kestell Cornish (unpubl. journal, 1876) mentions a coastal town by the name of Manahara, which is located north of the Masoala Peninsula, between the towns of Manakana and Bemarivo, and which is closer in spelling to "Manahare". Both *Paretroplus polyactis* and members of *Paratilapia* (the other freshwater species described by Bleeker (1878) was *Paracara* [now *Paratilapia*] *typus*) occur in this far northern region of the island where Audebert also collected, and the possibility remains that this more northerly location could represent the type locality. The type specimen of *Paracara typus* is in terrible condition and the illustration of *Paretroplus polyactis* lacks sufficient details that would permit one to associate these specimens to a particular geographic population. Given that *P. polyactis* occurs along nearly the entire eastern coastal region of Madagascar, and that differences between various populations spanning the geographic range of the species are subtle, the specific type locality is somewhat irrelevant given that a single species is recognized herein under the concept of *P. polyactis* (but see Discussion and Relationships below regarding intraspecific variation).

Eschmeyer (2006) reports that there are two syntypes for *P. polyactis*, one corresponding to RMNH 4478; the other is not provided an RMNH catalog number. An

Fig. 30. *Paretroplus polyactis*, UMMZ 239529, 163.8 mm SL; southeastern Madagascar: Fianarantsoa Province: Farafangana market.

examination of RMNH 4478 shows that this specimen is a juvenile *P. damii*, and there is reason to believe that this individual is probably a syntype of that species (see Notes on Type Series above for *P. damii*). The other putative syntype could not be located at RMNH and is presumed lost. Given Bleeker's (1878) detailed description and accompanying illustration, it is clear that he was not describing an amalgam of two different

Fig. 31. *Paretroplus polyactis*, AMNH 238569, 130.0 mm SL; northeastern Madagascar: Toamasina Province: Maroansetra market.

Fig. 32. *Paretroplus polyactis*, UMMZ 239527, 57.0 mm SL, illustrating strongly banded juvenile pigmentation pattern.

species (i.e., *P. polyactis* and *P. damii*), and it is unclear why Eschmeyer associated RMNH 4478 with *P. polyactis*. The distinctive lateral barring pattern in combination with dark scale margins and body shape of the specimen illustrated (Bleeker, 1878: fig. 2) are significantly different from that of *P. damii*. Also, the dorsal- (XVI spines and 17–19 rays) and anal-fin (13–16 rays) counts and lateral line scale count (32 or 33) provided for *P. polyactis* by Bleeker (1878) all fall outside the range of *P. damii* (table 2; also see Bleeker, 1868). Moreover, an old label in the jar with RMNH 4478 states "type" under the species name of "*Paretroplus dami*". Thus, both of the syntypes of *P. polyactis* described by Bleeker must be presumed lost.

MATERIAL EXAMINED: AMNH 88016, 19 ex., 112.9–191.8 mm SL; eastern Madagascar: Fianarantsoa Province: Mananjary: estuary of Mananjary River behind marketplace, ca. 1 km from sea: 21°05′S, 48°27′E; local fishermen, M. L. J. Stiassny, and P. N. Reinthal, 30-VI-1988. AMNH 88040, 3 ex., 124.5–152.5 mm SL; Fianarantsoa Province: Mananjary River, 1km from sea: 21°05′S, 48°27′E; M. L. J. Stiassny and P. N. Reinthal, 2-VII-1988. AMNH 88078, 1 ex., 132.6 mm SL; eastern Madagascar: Toamasina Province: ferry at Marosiky: 19°40′S, 48°50′E; M. L. J. Stiassny and P. N. Reinthal, 8-VII-1988. AMNH 88091, 10 ex., 72.3–149.7 mm SL; eastern Madagascar: Toamasina Province: Pangalanes Canal north of Mangoro River, Mahanoro town behind Hotel de la Pangalane: 19°55′S, 48°50′E; M. L. J. Stiassny and P. N. Reinthal, 8-VII-1988. AMNH 88116, 9 ex., 48.5–188.8 mm SL; eastern Madagascar: Toamasina Province: Toamasina, main marketplace in town center, caught nearby: 18°10′S, 49°25′E; local fishermen, M. L. J. Stiassny, and P. N. Reinthal, 15-VII-1988. AMNH 88135, 4 ex., 97.0–155.9 mm SL; eastern Madagascar: Toamasina Province: Ivoloina River at large bridge on Toamasina to Fenoarivo road, estuary: 18°00′S, 49°25′E; M. L. J. Stiassny and P. N. Reinthal, 15-VII-1988. AMNH 88139, 1 ex., 41.2 mm SL; eastern Madagascar: Toamasina Province: bridge over Canal de Pangalanes on Toamasina to Fenoarivo road, ca. 25km north of

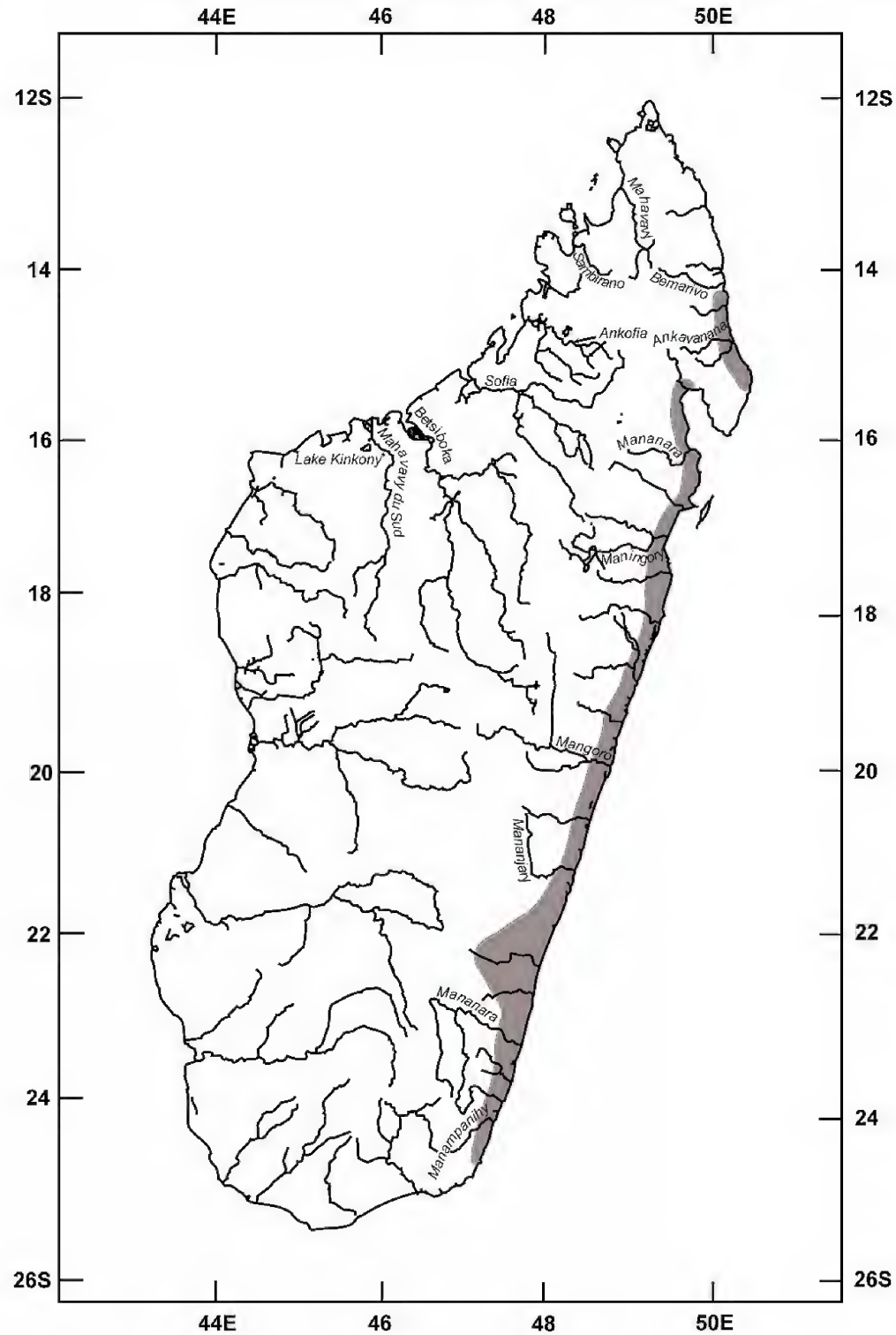


Fig. 33. Drainage map of Madagascar illustrating the geographic range for *P. polyactis*, the only species of *Paretroplus* that is restricted to eastern drainages and that occurs in southern basins. This distribution should be regarded as an approximation, given that the northern and southern range extent of *P. polyactis* remain uncertain (see Sparks and Stiassny, 2003; Sparks, 2004).

TABLE 3
Morphometric and meristic data for *Paretroplus polyactis*. For meristics, numerals in parentheses indicate number of specimens examined with that count. Syntypes for *P. polyactis* are presumed lost (see text).

	P. polyactis			
Character	N	Range	Mean	SD
Standard length (mm)	20	49.5–183.8	123.1	
Percentage of SL				
Head width (max.)	20	14.8–18.4	16.1	0.89
Head length	20	29.4–34.2	30.9	1.28
Body depth	20	48.9–58.9	54.9	2.67
Caudal peduncle length	20	6.8–10.1	8.2	0.91
Caudal peduncle width	20	3.7–5.8	4.7	0.56
Caudal peduncle depth	20	14.6–17.1	15.9	0.62
Pectoral-fin length	20	20.9–24.9	22.3	0.99
Pelvic-fin length	20	19.4–23.0	21.2	0.99
Last dorsal spine length	18	14.2–16.3	15.1	0.65
Percentage of HL				
Snout length	20	33.2–50.3	44.3	4.37
Orbit diameter	20	25.0–38.5	28.7	3.18
Upper jaw length	20	24.5–29.6	28.1	1.31
Lower jaw length	20	33.7–37.5	36.0	0.90
Interorbital width	20	31.4–35.2	33.6	1.04
Preorbital depth	20	22.5–34.1	30.3	2.89
Caudal peduncle length/width	20	1.3–2.2	1.8	0.26
Caudal peduncle length/depth	20	0.4–0.7	0.5	0.06
Scales in lateral line	20	31 (2), 32 (5), 33 (5), 34 (5), 35 (2), 36 (1)		
Scales: lateral line to dorsal fin	20	6 (15), 6.5 (1), 7 (4)		
Gill rakers (lower limb 1st arch)	20	11 (3), 12 (15), 13 (2)		
Vertebrae (precaudal + caudal)	18	15 + 16 =31 (3), 15 + 17 = 32 (13), 15 + 18 = 33 (2)		
Dorsal fin	19	XVI 17 (2), XVI 18 (4), XVII 16 (4), XVII 17 (6), XVII 18 (1), XVIII 15 (1), XVIII 16 (1)		
Anal fin	19	VII 14 (1), VIII 14 (4), VIII 15 (4), IX 13 (2), IX 14 (6), IX 15 (1), X 13 (1)		

Toamasina: 18°00′S, 49°25′E; M. L. J. Stiassny and P. N. Reinthal, 16-VII-1988. AMNH 88152, 1 ex., 95.4 mm SL; eastern Madagascar: Toamasina (= Tamatave) Province: Canal de Pangalanes on Toamasina to Fenoarivo (= Fenerive) road, ca. 100 m from outflow to sea: 18°00′S, 49°25′E; M. L. J. Stiassny and P. N. Reinthal, 17-VII-1988. AMNH 97003, 2 ex., 79–104 mm SL; eastern Madagascar: Toamasina Province: east of road by Salehy village, 1 km south of turnoff from Marolambo-Mananjary road: bay lake behind first dune about 100 m from sea: 19°55′S, 48°50′E; M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 16-IX-1990. AMNH 97006, 1 ex., 49.0 mm SL; data as for AMNH 97003. AMNH 97013, 7 ex., 71.5–103.2 mm SL; eastern Madagascar: Toamasina Province: Mahanoro market behind Hotel de la Pangalane: 19°55′S, 48°50′E; local fishermen, M. L. J. Stiassny, and P. N. Reinthal, 16-IX-1990. AMNH 97031, 2 ex., 52–55 mm SL; eastern Madagascar: Toamasina Province: mouth of Mangoro River opposite camp by Salehy village: 19°55′S, 48°50′E; M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 17-IX-1990. AMNH 97054, 1 ex., 109 mm SL; eastern Madagascar: Toamasina Province: Mangoro River drainage: Savalany River (small stream) by Ambodisovoka village at bridge over road to Marolambo; M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 18-IX-1990. AMNH 98171, 3 ex., 2 ex. C&S, 65.5–113.8 mm SL; eastern Madagascar: Toamasina Province: east of road by Salehy village,

1 km south of turnoff from Marolambo-Mananjary road: bay lake behind first dune about 100 m from sea: 19°55′S, 48°50′E; M. L. J. Stiassny, P. N. Reinthal, and G. J. P. Naylor, 17-IX-1990. AMNH 231359, 7 ex., 41.0–84.0 mm SL; northeastern Madagascar: Antsiranana Province: Sambava-Andapa Region: Lake Andohabeobe: ca. 7 km south of Sambava; PVL-99-01; P. V. Loiselle, 20-X-1999. AMNH 233656, 4 ex., 87.8–97.8 mm SL; northeastern Madagascar: Antsiranana Province: Andranory River: main channel of small coastal river just south of the airport at Antalaha; PVL-03-05; P. V. Loiselle. AMNH 238558, 3 ex., 128.5–185.0 mm SL; northeastern Madagascar: Toamasina Province: Antainambalana River: north (upriver) of town of Maroansetra: 15°25′5.4″S, 49°40′17.4″E; JSS 2-2003; local fishermen, J. S. Sparks, W. L. Smith, and K. L. Tang, 8-XI-2003. AMNH 238569, 7 ex., 1 ex. C&S, 100.0–130.0 mm SL; northeastern Madagascar: Toamasina Province: Maroansetra market: 15°25′ 60″S, 49°43′60″E; JSS 26-2003; J. S. Sparks, W. L. Smith, and K. L. Tang, 24-26-XI-2003. UMMZ 199407, 3 ex. (formerly MNHN 60-222), 84–116 mm SL; Madagascar. UMMZ 235015, 8 ex., 104–215 mm SL; southeastern Madagascar: Fianarantsoa Province: Mananjary market and port: 21°13′0″S, 48°19′60.0″E; JSS 94-26; J. S. Sparks and K. J. Riseng, 23-VIII-1994. UMMZ 235016, 18 ex., 3 ex. C&S, 46–220 mm SL; southeastern Madagascar: Fianarantsoa Province: Farafangana market: 22°49′0″S, 47°49′60.0″E; JSS 96-3; J. S. Sparks and K. J. Riseng, 1996. UMMZ 235017, 22 ex., 1 ex. C&S, 68–197 mm SL; southeastern Madagascar: Fianarantsoa Province: south of Farafangana: Manombo Special Reserve: 22°57′S to 23°08′S, 47°36′E to 47°48′E; PNR 96-2; P. N. Reinthal, 1996. UMMZ 236593, 1 ex., 84 mm SL; northeastern Madagascar: Antsiranana Province: east coast of Masoala Peninsula: Projet Masoala site 1006: mangrove swamp near Lalona river: 15°23′11.0″S, 50°26′24.0″E; JSS 94-49; J. S. Sparks and K. J. Riseng, 4-X-1994. UMMZ 238459, 7 ex., 1 ex. S, 95–190 mm SL; southeastern Madagascar: Fianarantsoa Province: Farafangana market: 22°49′0″S, 47°49′60.0″E; JSS 94-MKT-2-2; J. S. Sparks, K. J. Riseng, and P. N. Reinthal, 1994. UMMZ 238475, 1 ex., 108 mm SL; southeastern Madagascar: Fianarantsoa Province; JSS 94-MKT-4-1; J. S. Sparks and K. J. Riseng, 1994. UMMZ 238477, 1 ex., 84 mm SL; southeastern Madagascar: Fianarantsoa Province; JSS 94-MKT-1-1; J. S. Sparks, K. J. Riseng, and P. N. Reinthal, 1994. UMMZ 239527, 5 ex., 1 ex. C&S, 45.5–124.0 mm SL; southeastern Madagascar: Fianarantsoa Province: Andriambondro River (tributary of Rienana River): 6 km north of Karianga at town of Mahavelo: 22°21′47.0″S, 47°22′5.0″E: alt. 234.7m a.s.l.; JSS 96-5; J. S. Sparks and K. J. Riseng, 17-VI-1996. UMMZ 239528, 4 ex., 84–114 mm SL; northeastern Madagascar: Toamasina Province: Maroansetra market: 15°26′3.0″S, 49°44′29.0″E; JSS 94-39; J. S. Sparks and K. J. Riseng, 21-IX-1994. UMMZ 239529, 4 ex., 127–167 mm SL; southeastern Madagascar: Fianarantsoa Province: Farafangana market: 22°49′0″S, 47°49′60.0″E; JSS 94-MKT-5; J. S. Sparks, K. J. Riseng, and P. N. Reinthal, 18-VI-1994. UMMZ 239563, 3 ex., 102–154 mm SL; southeastern Madagascar: Fianarantsoa Province: south of Farafangana: Manombo Special Reserve: 22°57′S to 23°08′S, 47°36′E to 47°48′E; PNR 96-3; P. N. Reinthal, 1996.

DIAGNOSIS: *Paretroplus polyactis* is distinguished from congeners by a unique chain-link (diamond mesh) pigmentation pattern, owing to contrasting dark scale margins and light centers over the entire flank and portions of the head. It is also the only member of the genus in which the entire series of lateral bars is both strongly pigmented and spotted (not solid), due to more darkly pigmented scale margins than centers, regardless of size (e.g., vs. bars prominent and solid in *P. maromandia*). In life, *P. polyactis* is unique among deep-bodied members of the genus (Clade I) in possessing a bright red iris, a feature shared only with the elongate *P. lamenabe* (Clade F).

DESCRIPTION: Morphometric and meristic data presented in table 3. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in fig. 24A and 30–32. A deep-bodied, laterally compressed *Paretroplus* belonging to Clade I, which comprises all deep-bodied and more or less disk-shaped members of

Paretroplus (also including *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*) (fig. 1). Head shape ranges from pointed, not blunt, and only moderately steeply sloping in lateral view, to relatively blunt and somewhat steeply sloping (see Discussion and Relationships below). Snout ranges from mostly straight to moderately convex in lateral view. Specimens with convex snout characterized by indentation posterior to premaxillary pedicels, which may be quite pronounced. Predorsal profile mostly straight to moderately rounded. Caudal peduncle short, deep, and laterally compressed. No sexually dimorphic characters apparent, although unpaired fins of males slightly more elongate and pointed distally than females of comparative standard length.

Total vertebral count 31–33 (mode 32), with formulae of: 15 + 16, 15 + 17, 15 + 18 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, remaining upper-jaw teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, and only slightly reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw usually number five to eight on each side, and total 11–15. Teeth in lower jaw number four or five on each side, and total eight or nine. Upper- and lower-jaw teeth generally widely set and regularly spaced, although some teeth may be irregularly spaced and closely set.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. LPJ well sutured, with numerous interdigitating sutures on posteroventral margin. Seven to nine robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. In some specimens, bases of tooth plates becoming confluent or fused. Tooth plates not confluent with outer-row gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Anteromedial teeth on third pharyngobranchial tooth plates enlarged and robust, but not becoming molariform. Dentition on second pharyngobranchial tooth plates hooked and bicuspid and arrayed in two or three rows.

Eleven to 13 (mode 12) elongate, triangular gill rakers arrayed along lower limb of first gill arch. These rakers range from weakly to strongly denticulate, with few to many conical teeth dorsomedially. All other lower-limb rakers (i.e., those on gill arches 2–4) short, spherical, and strongly denticulate dorsally. Teeth on rakers of gill arches 2–4 elongate, conical and curved near crown, and as long or longer than raker bases. Epibranchial rakers on first gill arch elongate, numbering 10–13.

Body covered with large, regularly imbricate, cycloid scales. Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from both spiny and soft portions of dorsal and anal fins. Pelvic axillary scale present and well developed (fig. 23A). Interpelvic scale series well developed, terminal scale in series robust, elongate, and pointed distally. Lateral-line scales number 31–36 (mode 33). Chest scales somewhat smaller than other body scales, but not greatly reduced in size except anteroventrally. Anteroventral chest scales markedly reduced in size and embedded. Belly scales along ventral midline also markedly reduced in size and embedded. Four to six rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly 2/3 to 3/4 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XVI–XVIII spines, 15–18 soft rays. Anal with VII–X spines, 13–15 soft rays. Origin of dorsal fin ranges from about level of to slightly posterior to vertical

through pectoral-fin insertion. Caudal fin emarginate, trailing margins of upper and lower lobes weakly produced (compared to other deep-bodied members of genus) in larger individuals. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins produced and pointed in larger specimens. Pelvic fin extending just to anal-fin origin in smaller specimens, and in larger individuals pelvic fin ranging from not quite reaching anal-fin origin to extending well beyond origin when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital excavations present. Paired anterior gas bladder bullae with tough, thickened tunica externa and narrow tubular connections (= diverticula) to main gas bladder chamber (fig. 20B). Anteriormost chambers firmly lodged in exoccipital recesses. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital (fig. 20B). Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins. Modified "prezygopophyses" present on anterior neural arches (fig. 18D).

Coloration in Life: Base body coloration pale yellow, olive, or golden brown, and becoming pale salmon in sexually active individuals. Body pale yellow to pale olive ventrally. Strong chain-link (diamond mesh) pigmentation pattern on flanks and dorsoposterior portion of head, owing to contrasting dark scale margins and light centers (see de Rham and Nourissat, 2004: 84–87). Seven to nine prominent black vertical bars present on flank from posterior margin of opercle to caudal-fin base. Populations from Mananjary northward possess eight or nine lateral bars, whereas those along the southeastern coast and inland from about Karianga and Farafangana (22°S) southward have seven lateral bars. Head region generally darker than flanks, but with same pale yellow, olive, or golden brown coloration. Opercle and cheek frequently with some iridescent bright golden patches. Upper lip, interorbital region, lacrimal, and snout grayish brown to uniform dark brown. Iris of eye bright red, which gives species its Malagasy name *masovoatoaka*, which translates as "eyes bloodshot from drinking (rum)". Lower lip, gular region, anterior chest, belly, interopercle, and ventral cheek white, pale yellow, or light olive. Unpaired fins dark gray, charcoal, or black, with dark red margins. Pectoral fins range from hyaline to translucent brown or black. Pelvic fins dark gray to black, with light gray to whitish leading edge. Juveniles to about 60 mm SL with well-differentiated lateral bars that extend vertically over entire flank. Although still prominent, lateral bars become wider and less well differentiated in adults.

Coloration in Preservative: Base body coloration ranges from pale yellow, to olive, to dark brown. Seven to nine prominent dark brown or charcoal vertical bars present on flank from posterior margin of opercle to caudal-fin base. In general, populations from Mananjary northward have eight or nine lateral bars (figs. 24A and 31), whereas those from about Karianga and Farafangana (about 22°S) southward have only seven lateral bars (fig. 30). Pigmentation pattern of dark scale margins and lighter centers, including scales on lateral bars, creates chain-link pattern over entire flank and portion of head. Body generally somewhat lighter overall dorsally. Interorbital region, lacrimal, and snout pale grayish yellow to uniform dark brown. Upper lip charcoal to dark grayish brown, and lower lip pale yellow to golden brown. Gular region, anterior chest, belly, interopercle, and ventral cheek grayish yellow to golden brown. Dorsal and anal fins range from dark brown, to dark grayish brown, to gray distally and black terminally. Caudal fin ranges from pale yellow anteriorly and charcoal posteriorly, to dark brown or dark grayish brown. Pectoral fins pale yellow, olive, or light brown. Pelvic fins range from pale yellow anteriorly and charcoal posteriorly, to dark grayish brown. Juveniles to about 60 mm SL with distinctive narrow and well-separated bars that extend vertically over entire flank (fig. 32); in adults bars

remain prominent, but becoming less well differentiated and more broad, as well as less strongly pigmented ventrally.

DISTRIBUTION AND HABITATS: *Paretroplus polyactis* exhibits an extensive latitudinal range spanning nearly the entire eastern coast of Madagascar (fig. 33). The known range for the species extends from somewhat north of the Masoala Peninsula, the Lokoho River at Ambatoloaka (de Rham and Nourissat, 2004: 84), southward to the Manampanihy River, located 20 km inland of Fort Dauphin. Interestingly, although *P. polyactis* is primarily a coastal species throughout most of its range, frequently inhabiting estuarine and brackish habitats and generally not straying far inland, de Rham and Nourissat (2004: 85) report that the species is absent from coastal areas at the southern limit of its range near Fort Dauphin, where it is restricted to the upper reaches of the Manampanihy River. The most southern coastal populations of *P. polyactis* known occur at Manombo (including rivers and streams within Manombo Special Reserve) and Vangaindrano, which are located to the south of Farafangana. The species has also been collected about 60 km inland from the sea in the Andriambondro River (tributary of Rienana River) just to the north of Karianga (22°21′47″S, 47°22′05″E) (J. Sparks, personal obs.). Of the other endemic cichlid species, only *Ptychochromis grandidieri* exhibits a latitudinally extensive north-south geographic range, although the species does not extend nearly as far north (restricted to the south of the Makira Protected Area) as *P. polyactis*, whereas its southern range limit remains uncertain (see Stiassny and Sparks, 2006: fig. 1).

Considering the extensive latitudinal range of *P. polyactis* and that the species can tolerate brackish conditions, the species does not appear to be in immediate danger of extinction. Nevertheless, it is important to note that this species is highly prized as a food fish by the Malagasy, commanding a high price in markets, and is heavily targeted by fishermen throughout eastern Madagascar. Anecdotally, over the past decade many researchers, including our group, our Malagasy colleague Noramalala Raminosoa (University of Antananarivo), Paul Loiselle (WCS/NY Aquarium), and de Rham and Nourissat (2004), have noticed both a decline in abundance as well as a decline in size of *P. polyactis* offered for sale in markets throughout eastern Madagascar. Of all the species of *Paretroplus*, with the possible exception of *P. damii*, which is widely distributed throughout northwestern and northern Madagascar, *P. polyactis* currently appears to be the least threatened (see Relationships and Discussion below). It is frequently found in quite degraded habitats and I have even observed the species swimming in seawater off of mangrove swamps during high tide. If the current rate of habitat destruction throughout eastern Madagascar is not slowed, the status of *P. polyactis* could rapidly change.

LOCAL NAME: The iris of the eye is bright red in *P. polyactis*. *Masovoatoaka*, which translates as "eyes bloodshot from drinking (rum)", is the Malagasy name used to refer to *P. polyactis* throughout its range.

ETYMOLOGY: The specific name *polyactis* derives from *poly-* (Greek: *polus*, meaning "many") and *actis* (Greek: "ray, sunbeam, beam of light"), most likely in reference to the reddish, orange, and brown coloration of the species, which is quite striking in life.

RELATIONSHIPS AND DISCUSSION: *Paretroplus polyactis* is a member of Clade I, comprising all of the deep-bodied members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*) (fig. 1), which is supported by three unambiguously optimized morphological features, the first two of which are unique and unreversed: a deep and essentially disk-shaped body (fig. 24A), lateral ridges of scales ("scale sheathing") along the bases of the soft dorsal and anal fins that are free from the fin membranes over their entire length, and the presence of seven to nine prominent lateral bars (figs. 30–32).

Paretroplus polyactis is recovered as the sister taxon to Clade J, which includes all deep-bodied members of the genus with distributions restricted to western basins (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*) (fig. 1). *Paretroplus polyactis* lacks the following derived anatomical features that unite members of Clade J: a blunt snout, with a steeply sloping profile in

lateral view, and a distinctive lateral striping pattern of alternating light and dark horizontal stripes extending from the anterior margin of the orbit to origin of the caudal fin. A recent study using only nucleotide characters from multiple mitochondrial and nuclear genes recovered *P. polyactis* in a slightly different position, as the sister taxon to a clade comprising *P. kieneri* and Clade J (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*) (Sparks and Smith, 2004: fig. 1).

In addition to its unique chain-link pigmentation pattern, *P. polyactis* is distinguished from all congeners, except *P. lamenabe*, by the presence of a bright red iris in life. However, the iris is not nearly as bright red in *P. lamenabe*. It is the only member of *Paretroplus* in which the lower-jaw teeth at the symphysis of the left and right dentaries are only slightly reduced in size (all other species exhibit symphyseal teeth greatly reduced in size). *Paretroplus polyactis* can usually be distinguished from other members of Clade I by the number of gill rakers on the lower limb of the first arch (11–13 [mode 12] in *P. polyactis* vs. 9–10 in other members of Clade I; two individuals of *P. maculatus* were examined with 11 lower-limb gill rakers). In addition, *P. polyactis* can generally be distinguished from other deep-bodied *Paretroplus* (Clade I) by the distribution of accessory parapophyses on the caudal vertebral centra. *Paretroplus polyactis* usually has accessory parapophyses restricted to the first two caudal vertebral centra, but these structures are occasionally also present on the third caudal centra, whereas all other deep-bodied members of the genus always have parapophyses on at least the first three caudal vertebral centra (e.g., *P. dambabe* has parapophyses on the first three or four caudal vertebral centra, and *P. maromandia*, *P. maculatus*, and *P. menarambo* on the first four or five caudal vertebral centra). These accessory parapophyses directly support the upper wall of the paired posterior gas bladder chambers.

Interestingly, variation in nucleotide sequences between populations of *P. polyactis* from Mananjary along the southeastern coast and Maroansetra in the northeast is about the same as between other pairs of *Paretroplus* that are recognized as distinct species (e.g., *Paretroplus dambabe* and *P. maculatus*) and even greater than that observed between *P. nourissati* and *P. tsimoly* (Sparks and Smith, 2004). Nevertheless, I am unable to find consistent (invariable) morphological features within any of the populations of *P. polyactis* spanning the eastern coast of Madagascar (from north of the Masoala Peninsula to the far south of the island) that would indicate the presence of more than a single species.

For example, in general populations from Mananjary (southeast coast) northward have eight or nine lateral bars (figs. 24A and 31), whereas those from approximately Karianga and Farafangana southward (i.e., from about 22°S) have only seven lateral bars (fig. 30). Northern populations seem to differ from central and southern populations in head shape, with northern populations (Maroansetra and northward) exhibiting a more blunt head and less pointed snout (and generally more rounded and disk-shaped body) (fig. 31). The head is noticeably more pointed in populations south of Maroansetra and the Masoala Peninsula (fig. 30). In these populations the snout is generally convex, and there is a prominent indentation posterior to the premaxillary pedicels. In other words, if one looks across the range of *P. polyactis* anatomical differences between various populations are evident (in both juveniles and adults); however, there is no clear geographic break where the various morphotypes align. Clearly more data (in particular molecular phylogenetic studies) are needed regarding population structure of *P. polyactis* throughout its extensive range along the eastern coast of Madagascar before any hypotheses of species boundaries can be tested.

Paretroplus petiti Pellegrin, 1929
Figures 34–35; plate 1C; table 4

HOLOTYPE: MNHN 1928.282, 82.8 mm SL; northwestern Madagascar: Province of Mahajanga (Majunga): Riviere de Maintimaso; G. Petit.

DIAGNOSIS: Based on the holotype, a juvenile, and only known specimen. *Paretroplus petiti* is a deep-bodied *Paretroplus* and a member of Clade I. It is distinguished from

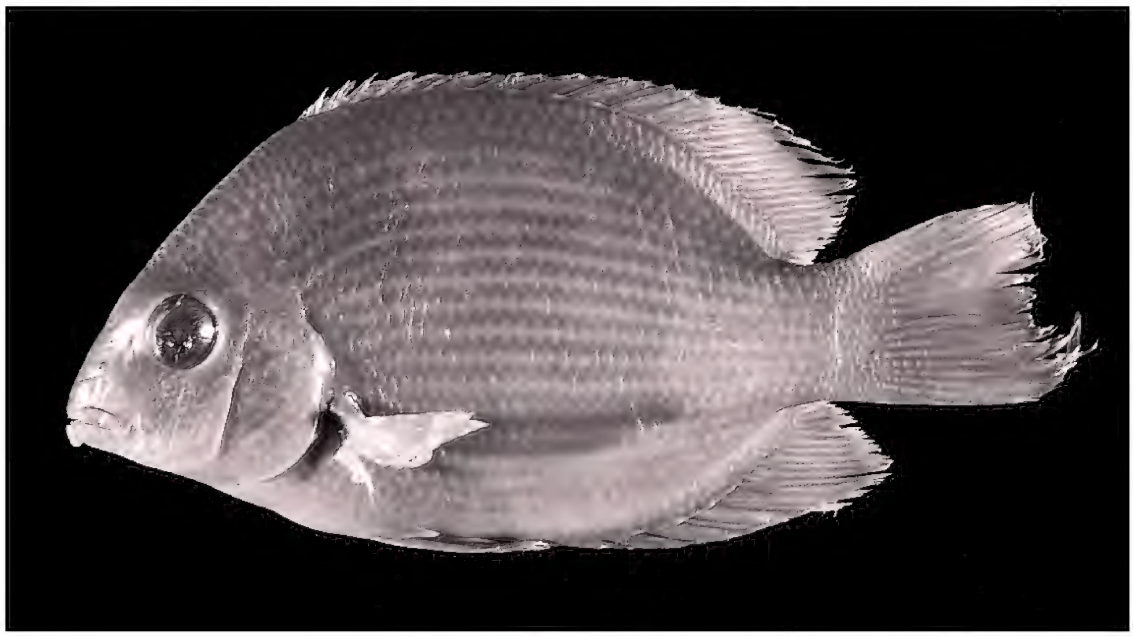


Fig. 34. *Paretroplus petiti*, holotype, MNHN 1928.282, 82.8 mm SL; northwestern Madagascar: Mahajanga (Majunga) Province: Maintimaso River.

all other members of this clade, except *P. menarambo*, by dark brown coloration in combination with the lack of a strong lateral barring pattern. It is distinguished from *P. menarambo* by the absence of a pinstriped pigmentation pattern (in preservation), which results in the latter species due to conspicuous spotting on scales. *Paretroplus petiti* can be distinguished from all congeners not included in Clade I by a deep, disk-shaped body and the presence of lateral ridges of scales ("scale sheathing") that are free from the fin membranes over the entire length of the soft dorsal and anal fins. It should be noted that this diagnosis is tentative in that it is based on a single juvenile specimen and that live coloration is not known (i.e., lack of distinguishing marks could be an artifact of long-term preservation).

DESCRIPTION: (Note: The following description is based on features that can be visualized (including radiographically) in the intact holotype, the only known specimen, without causing damage to the specimen.) Morphometric and meristic data presented in table 4. Morphological characteristics and general pigmentation pattern in preservative can be observed in figure 34. A deep-bodied, laterally compressed *Paretroplus* belonging to Clade I, which comprises all deep-bodied and essentially disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. polyactis*) (fig. 1). Head relatively blunt and steeply sloping in lateral view. Snout mildly convex. Predorsal profile mostly straight and only slightly rounded. Caudal peduncle short, deep, and laterally compressed.

Total vertebral count 33, with a formula of 15 + 18 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate, unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, remaining teeth graded in size laterally. Lower-jaw damaged and counts not possible. Teeth in upper jaw number six on one side and seven on the other, and total 13. Upper- and lower-jaw teeth widely set.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Nine elongate and triangular gill rakers arrayed along lower limb of first gill arch. Rakers

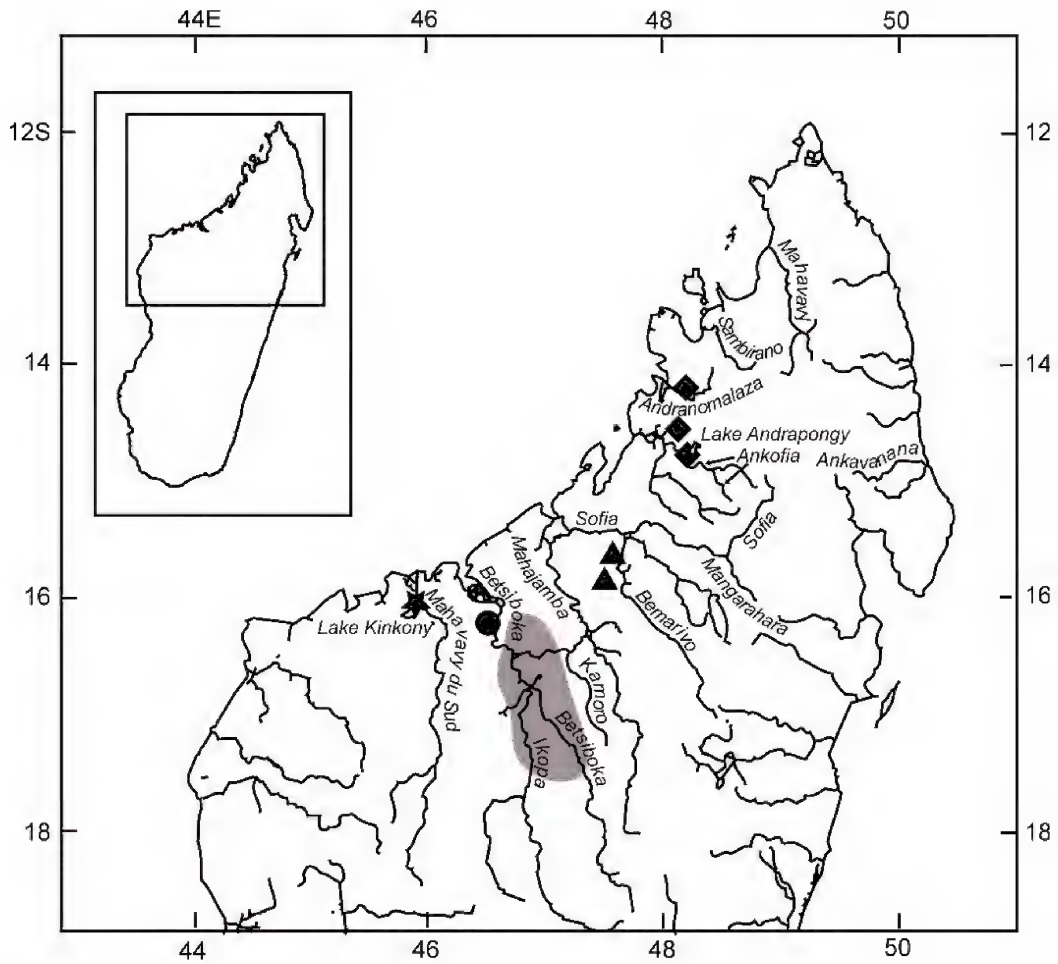


Fig. 35. Drainage map of northern Madagascar illustrating the hypothesized type locality for *Paretroplus petiti* (solid circle; see Sparks, 2002, for a discussion) and the known geographic ranges for the other members of Clade J, *P. maculatus* (gray shading), *P. menarambo* (triangles), *P. maromandia* (diamonds), and *P. dambabe* (star).

appear edentate in holotype (but difficult to determine on intact specimen). All other lower-limb rakers (i.e., those on gill arches 2–4) short and strongly denticulate dorsally. Epibranchial rakers on first gill arch elongate.

Body covered with large, regularly imbricate, cycloid scales. Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from both spiny and soft portions of dorsal and anal fins. Pelvic axillary scale present and well developed. Interpelvic scale elongate, robust, and rounded distally. Lateral-line scales number 39. Chest scales only slightly smaller than lateral body scales and weakly embedded. Belly scales small compared to other body scales and strongly embedded, those along ventral midline smallest. Five (left) to six (right) rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Preopercle scaled (including shaft) except ventrally. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly 2/3 to 3/4 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XVII spines, 18 soft rays. Anal with IX spines, 14 soft rays. Origin of dorsal fin at about level of vertical through

TABLE 4
Morphometric and meristic data for holotype of *Paretroplus petiti*.

Character	*P. petiti*
Standard length (mm)	82.8
Percentage of SL	
Head width (max.)	17.6
Head length	30.7
Body depth	57.9
Caudal peduncle length	6.8
Caudal peduncle width	5.3
Caudal peduncle depth	17.2
Pectoral-fin length	23.3
Pelvic-fin length	24.0
Last dorsal spine length	16.8
Percentage of HL	
Snout length	41.3
Orbit diameter	34.3
Upper jaw length	28.0
Lower jaw length	36.2
Interorbital width	36.6
Preorbital depth	30.7
Caudal peduncle length/width	1.3
Caudal peduncle length/depth	0.4
Scales in lateral line	39
Scales: lateral line to dorsal fin	7
Gill rakers (lower limb 1st arch)	9
Vertebrae (precaudal + caudal)	15 + 18 = 33
Dorsal fin	XVII 18
Anal fin	IX 14

pectoral-fin insertion. Caudal fin emarginate, but damaged terminally. Pectoral fin broad and rounded at distal margin. Pelvic fins extending beyond anal-fin origin, to about level of third anal-fin spine, when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital excavations present. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

Coloration in Life: Unknown. Only known specimen is the formalin-fixed holotype. As in other deep-bodied members of *Paretroplus* restricted to western drainages (Clade J), it is clear that, in life, *P. petiti* is characterized by the presence of conspicuous alternating, light and dark horizontal stripes on the flank.

Coloration in Preservative: Base body coloration dark golden brown. Alternating dark (dark brown) and light (golden brown) horizontal striping pattern evident on flanks (fig. 34). Very faint horizontal barring pattern also evident on flanks, but hardly noticeable. No additional distinguishing markings present on flanks. Snout and interorbital region dark grayish brown. Otherwise, head region more or less a uniform dark brown. Unpaired fins golden brown to grayish brown. Spiny dorsal with black pigment along distal margin. Pectoral fins light golden brown. Pelvic fins grayish brown and golden brown.

Viscera and Diet: Based on examination of a radiograph of the holotype, the gut is packed with crushed shells, indicating that *P. petiti* is primarily a molluscivore.

Distribution and Habitats: There has been some uncertainty surrounding the type locality of *P. petiti* Pellegrin, 1929, which Pellegrin reports as "Rivière de Maintimaso (province de Majunga): G. Petit". From the limited amount of information that is available, it appears that the type specimen of *P. petiti* (MNHN 1928-282) was collected from the Maintimaso River, a tributary of the westward flowing Betsiboka River, near the town of Maintimaso (16°10′60″S, 46°43′00″E), which is situated roughly 69 km (37 nm) southeast of Majunga (= Mahajanga) in northwestern Madagascar (fig. 35). The MNHN database, however, reports the collection locality of this specimen as "Ambila". No town with this spelling could be located in the vicinity of Majunga, although a town with the name of Ambilo is located near the Betsiboka River, about 35 km (19 nm) south of Majunga and to the northwest of Maintimaso. To add to the confusion, an old tag with the species name and also including the word "Ambanja" was found in the jar with the holotype at the MNHN (Paris). Ambanja is a large town located several hundred km to the north of Mahajanga and Maintimaso. No additional

information with regard to either the Ambila or Ambanja localities could be located, and the most prudent course of action is to accept the locality information presented by Pellegrin (1929).

In response to this interpretation de Rham and Nourissat (2004: 102) note that they believe that "Ambanja" refers not to the large town located far to the north, but instead to Lake Ambanja, which is located near the town of Ambato-Boeni, which itself is located about 96 km (52 nautical miles) to the southeast of Mahajanga and also within the Betsiboka drainage basin. However, it seems that de Rham and Nourissat and their Malagasy colleagues never collected in Lake Ambanja, but instead in nearby Lake Marajory. From Lake Marajory they obtained specimens that they refer to as *P.* cf. *maculatus* (see discussions under *P. maculatus* and *P. menarambo* below), which are clearly referable to *P. maculatus* given their possession of a large, black humeral blotch. They also mention that their Malagasy colleague apparently collected another species of *Paretroplus* from the lake in 2003, but these specimens were lost due to attacks by bandits and export problems.

Despite this uncertainty, nevertheless, it is clear from the information that is available that the holotype of *P. petiti* was not collected from the Mahavavy du Sud drainage basin, to which *P. dambabe* is endemic, but instead was obtained from a tributary of the Betsiboka River, one of Madagascar's largest drainage basins (fig. 35). Although *P. dambabe* was only recently described (Sparks, 2002a), since at least the early 1960s individuals of this species collected from Lac Kinkony, a large floodplain lake located within the Mahavavy du Sud drainage basin, have erroneously been referred to *P. petiti* (e.g., Kiener, 1963; Kiener and Thérézien, 1963; Kiener and Maugé, 1966). Based on results presented by Sparks (2002a) and herein, all specimens previously assigned to *P. petiti* that were collected in Lac Kinkony are instead referable to *P. dambabe* (see Relationships and Discussion for *P. dambabe* below). Although the conservation status of *P. petiti* is unknown, the possibility remains that *P. petiti* is extant in the Betsiboka River drainage basin.

LOCAL NAME: Unknown.

ETYMOLOGY: Named in honor of G. Petit who collected the holotype that was described by Pellegrin (1929).

RELATIONSHIPS AND DISCUSSION: *Paretroplus petiti* is recovered as a member of Clade I, comprising all of the deep-bodied and more or less disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. polyactis*), which is supported by three unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1). Apart from differences in pigmentation pattern and coloration, all members of Clade I are morphologically very similar.

In the combined analysis of morphological features and nucleotide characters, *P. petiti* is recovered in an unresolved polytomy with all other deep-bodied species of *Paretroplus* that have distributions restricted to western basins (fig. 35: Clade J). Monophyly of Clade J, comprising *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*, is supported by two unambiguously optimized morphological features, the second of which is unique and unreversed: the presence of a blunt snout with a steeply sloping profile in lateral view and a distinctive lateral pigmentation pattern comprising alternating light and dark horizontal stripes. A lack of resolution within Clade J is due to the fact the *P. petiti* (known only from the formalin-fixed holotype) is included on the basis of morphological features only, which are insufficient for resolving relationships within this anatomically conservative clade.

Since at least the early 1960s, individuals that are now placed in *P. dambabe* Sparks, 2002 were erroneously referred to *P. petiti* (e.g., Kiener, 1963; Kiener and Thérézien, 1963; Kiener and Maugé, 1966). Based on the results presented by Sparks (2002a) and discussed above, all specimens previously assigned to *P. petiti* that were collected in Lac Kinkony, Mahavavy du Sud drainage basin, are determined instead to be members of *P. dambabe*, and *P. petiti* is, therefore, currently known only from the holotype described by Pellegrin (1929), presumably collected from the Betsiboka drainage basin.

Paretroplus petiti is readily distinguished from *P. dambabe* in preservative by overall coloration (dark brown vs. light yellow-olive in *P. dambabe*), the absence of dark brownish spotting on the flanks (present in *P. dambabe*), and a deeper body (57.9% SL vs. mean 52.8% [ranges from 48.3%–57.1%] in *P. dambabe*). Sparks (2002a) noted that the holotype of *P. petiti*, a juvenile, is not only considerably deeper bodied than *P. dambabe* of similar standard length, but deeper bodied than any individual of *P. dambabe* examined, whereas it is quite similar in body depth to specimens of *P. menarambo* of similar standard length.

As discussed in detail by Sparks (2002a), the possibility exists that *P. petiti* and *P. menarambo* Allgayer, 1996 are conspecific. Given that only a single juvenile of *P. petiti* (MNHN 1928-282, holotype) is known, Sparks (2002a) deferred judgment on the status of *P. menarambo* until more material from the region of the putative type locality of *P. petiti* became available for comparison. The holotype of *P. petiti* is well preserved in terms of pigmentation pattern, and is similar in body shape and pigmentation pattern, in preservation, to *P. menarambo* (fig. 21D), a species restricted to the Bemarivo River floodplain lakes within the Sofia River basin in northwestern Madagascar, and which until very recently was presumed extinct. *Paretroplus petiti* and *P. menarambo* are both dark brown with a conspicuous pattern of thin, alternating light and dark horizontal stripes on the flanks (figs. 21D and 34). In the original description of *P. petiti*, Pellegrin (1929) noted this horizontal striping pattern, unique to members of Clade J, yet did not mention any additional distinctive markings. Apart from *P. petiti* and *P. menarambo*, no other species within the genus are dark brown overall in preservative and lack additional distinctive lateral flank markings, with the exception of a faint vertical barring pattern. These vertical bars are very faint in the holotype of *P.petiti*, and although not mentioned by Pellegrin (1929) in the original description may have faded considerably over time in preservative. Whereas coloration in life for *P. petiti* is unknown, in life *P. menarambo* is characterized by a pinstriped lateral pigmentation pattern, a pattern which is still quite obvious (and distinctive) in preservative in many specimens (see de Rham and Nourissat, 2004: 98–100).

One final point merits mentioning. Deep-bodied members of *Paretroplus* that occur in northwestern Madagascar (Clade J) are narrowly endemic in distribution, and as far as is known, all are restricted to a single drainage basin (Sparks, 2002a, 2004a) and no two species occur sympatrically. *Paretroplus menarambo* was endemic to the Bemarivo River drainage basin, whereas the holotype of *P. petiti* was collected from the Betsiboka River drainage basin, assuming the collection locality reported by Pellegrin (1929) is correct. The Betsiboka and Bemarivo are not adjacent basins in northwestern Madagascar, which might cast doubt on the possibility that these two nominal taxa are conspecific.

Paretroplus kieneri Arnoult, 1960
Figures 36–38; plate 1D; table 5

Paretroplus cf. *kieneri* upper Kamoro River: de Rham and Nourissat, 2004: 111–112.

Paretroplus cf. *kieneri* Mahajamba River: de Rham and Nourissat, 2004: 111–112.

Paretroplus sp. of Lake Parinandrina: de Rham and Nourissat, 2004: 129–130.

HOLOTYPE: MNHN 1960-580, adult female, 122.8 mm SL; northwestern Madagascar: Mahajanga (= Majunga) Province: Mahavavy du Sud drainage basin: Lake Kinkony; A. Kiener.

PARATYPE: MNHN 1960-581, 1 ex., 117.7 mm SL; data as for holotype.

ADDITIONAL MATERIAL EXAMINED: AMNH 97363, 1 ex., 111.4 mm SL; northwestern Madagascar: Mahajanga Province: Mahavavy du Sud drainage basin: Lake Kinkony; P. V. Loiselle and local fishermen, 27-VI-1993. AMNH 229560, 2 ex., 1 ex. C&S, 99.9–100.5 mm SL; northwestern Madagascar: Mahajanga Province: Akalimilotrabe (= Akalimilotra) River, north bank tributary of Betsiboka River, at Maevatanana: 16°48′4.8″S, 47°0′34.2″E; P. V. Loiselle and local residents, 7-VI-1997. AMNH 238561, "chocolat", 6 ex., 1 ex. C&S (in part), 109.0–134.0 mm SL; northwestern Madagascar: Betsiboka River drainage basin: Kamoro River; JSS 35-2003; J.-C. Nourissat,

Fig. 36. *Paretroplus kieneri*, holotype, MNHN 1960-580, 122.8 mm SL; northwestern Madagascar: Mahajanga (= Majunga) Province: Mahavavy du Sud drainage basin: Lake Kinkony.

2003. AMNH 238560, "géant", 5 ex., 126.0–160.0 mm SL; northwestern Madagascar: Mahajanga Province: Mahajamba River; JSS 32-2003; J.-C. Nourissat, 2003. AMNH 238567, 1 ex. (dried), 94.0 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: Lake Parinandrina; JSS 33-2003; J.-C. Nourissat, 2003. MHNG 2537.41, 2 ex., 103.7–114.2 mm SL; Madagascar: northwest: P. de Rham and J.-C. Nourissat, X-1992. MHNG 2537.42, 1 ex., 111.8 mm SL; north-

Fig. 37. *Paretroplus kieneri* "géant", AMNH 238560, 146.2 mm SL, from Mahajamba River population, illustrating dark gray coloration on body and fins.

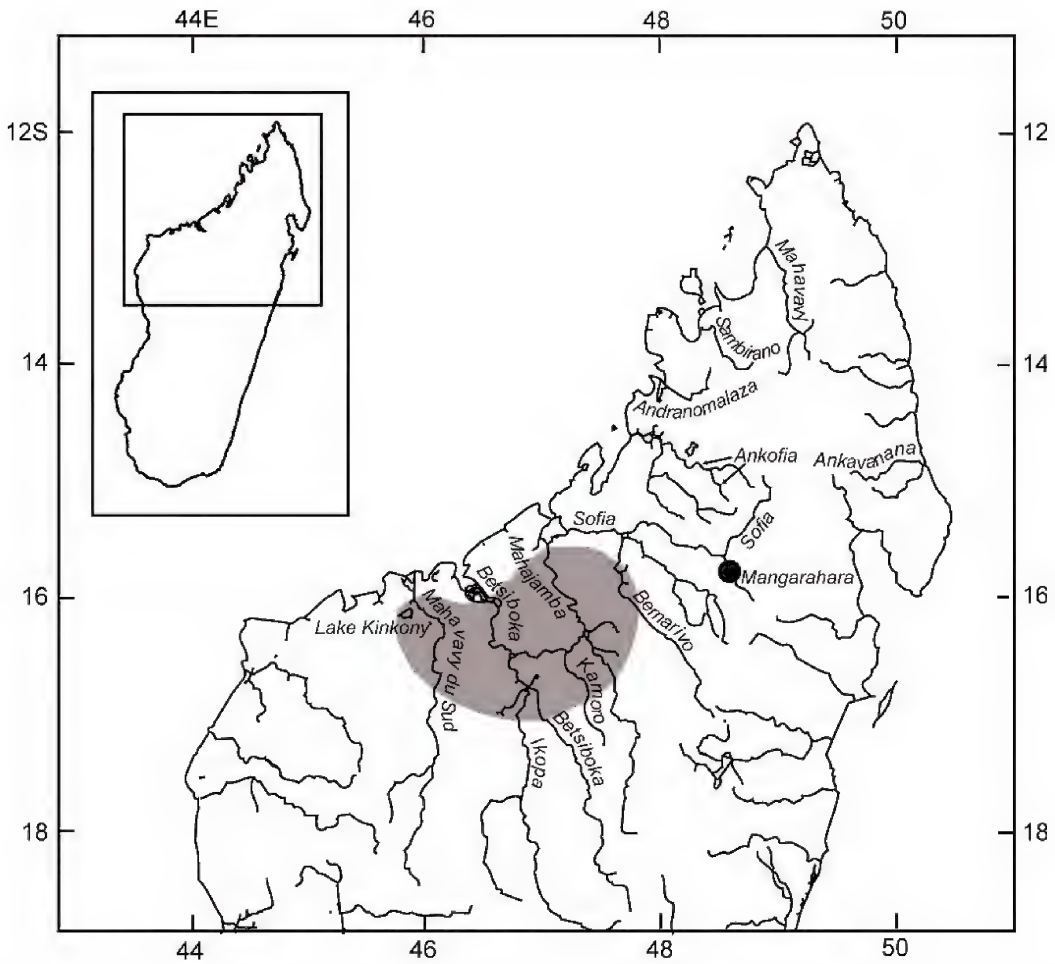


Fig. 38. Drainage map of northern Madagascar illustrating the geographic ranges for members of Clade H, *Paretroplus kieneri* (gray shading) and *P. gymnopreopercularis* (black circle), which should be regarded as approximations as many remote northwestern basins remain poorly surveyed (see Sparks and Stiassny, 2003; Sparks, 2004).

western Madagascar: Lac Sarodrano: 30 km north of Mampinkony: P. de Rham and J.-C. Nourissat, 22-X-1992. MHNG 2537.43, 3 ex., 1 ex. C&S, 102.5–105.7 mm SL; Madagascar: lac environment Boriziny (Port Berger): P. de Rham, X-II-1991. MNHN 1922-0175, 1 ex., 107.8 mm SL; northwestern Madagascar: Ambatomainty. MNHN 1922-0176, 1 ex., 86.3 mm SL, northwestern Madagascar: Ambatomainty. MNHN 1922-0177, 1 ex., 82.0 mm SL, northwestern Madagascar: Ambatomainty. MNHN 1922-0180, 1 ex., 40.5 mm SL; northwestern Madagascar: Ambatomainty. (Note: previous four specimens were misidentified as *P. damii* in the MNHN database.) MNHN 1960.581, 3 ex. (preserved in lot with paratype), 131.1–142.2 mm SL; northwestern Madagascar: Mahajanga Province: Mahavavy du Sud drainage basin: Lake Kinkony. MNHN 1966-1043, 13 ex.; northwestern Madagascar: Province of Majunga: Riviere Ankalamilotra. UMMZ 235018, 5 ex., 1 ex. C&S, 70–108 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: near Ampijoroa Forestry station: Lake Ravelobe: 16°18′31.0″S, 46°48′59.0″E; JSS 96-24; J. S. Sparks and K. J. Riseng, 14-VIII-1996. UMMZ 236592, 4 ex., 1 ex. C&S, 84–102 mm SL; northwest-

TABLE 5
Morphometric and meristic data for *Paretroplus kieneri*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

		P. kieneri			
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	25	122.8	68.7–158.8	109.8	
Percentage of SL					
Head width (max.)	25	14.9	14.9–18.1	16.2	0.90
Head length	25	27.7	26.1-31.2	29.1	1.13
Body depth	25	49.5	42.8–55.7	48.5	2.51
Caudal peduncle length	25	6.8	6.4–9.8	7.9	0.98
Caudal peduncle width	25	3.5	3.4–6.0	4.6	0.77
Caudal peduncle depth	25	17.3	14.7–18.0	16.1	0.70
Pectoral-fin length	24	23.8	20.7–26.6	22.9	1.16
Pelvic-fin length	25	22.7	21.5–24.5	23.0	0.81
Last dorsal spine length	7	18.3	14.7–18.3	15.9	1.26
Pre-dorsal length	22	38.1	38.1–45.2	43.3	1.51
Pre-anal length	22	57.3	52.2–59.6	55.5	2.02
Pre-pelvic length	22	41.5	34.6–42.6	38.1	1.84
Percentage of HL					
Snout length	25	37.9	36.0–45.1	40.9	2.73
Orbit diameter	25	30.9	27.5–36.5	31.5	2.01
Upper jaw length	25	29.1	23.2–30.1	27.0	1.56
Lower jaw length	25	32.4	28.7–36.6	32.0	1.64
Interorbital width	25	35.0	31.0–38.6	34.5	1.98
Preorbital depth	25	29.1	23.5–31.6	27.5	2.13
Caudal peduncle length/width	25	2.0	1.3–2.3	1.8	0.29
Caudal peduncle length/depth	25	0.4	0.4–0.6	0.5	0.06
Scales in lateral line	24	33 (1), 35 (1), 36 (2), 37 (6), 38 (10), 39 (3), 40 (1) (H)			
Scales: lateral line to dorsal fin	17	5 (1), 6 (16) (H)			
Gill rakers (lower limb 1st arch)	25	9 (17), 10 (8) (H)			
Vertebrae (precaudal + caudal)	30	15 + 17 = 32 (18) (H), 15 + 18 = 33 (8), 16 + 16 = 32 (3), 16 + 17 = 33 (1)			
Dorsal fin	30	XVIII 13 (1), XVIII 14 (7), XVIII 15 (1), XIX 13 (9), XIX 14 (9) (H), XX 13 (2), XX 14 (1)			
Anal fin	30	IX 12 (7), X 11 (13) (H), X 12 (8), XI 11 (1), XI 12 (1)			

ern Madagascar: Mahajanga Province: Mahavavy du Sud drainage basin: Lake Kinkony: 16°05′38.0″E, 45°51′37.0″E; JSS 94-15; J. S. Sparks and K. J. Riseng, 14-VII-1994. UMMZ 239565, 1 ex., 76 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: across from Ampijoroa Forestry station: Lake Ravelobe: 16°18′34.0″S, 46°48′59.0″E; JSS 94-10; J. S. Sparks and K. J. Riseng, VII-1994. UMMZ 240353, 2 ex. S, ca. 80 mm SL; northwestern Madagascar; received from L. de Mason II-1995.

DIAGNOSIS: A shallow-bodied *Paretroplus* distinguished from all congeners except *P. gymnopreopercularis* by the presence of a blotchy, mottled, and irregular (grayish, orange, olive, and brown) pigmentation pattern, the absence of vertical bars on the flanks, and by a fleshy snout that extends rostral to the lips and also ventrally to cover a portion of the upper lip. *Paretroplus kieneri* is distinguished from its sister taxon, *P. gymnopreopercularis*, by the presence of a more or less fully scaled preopercle, except along the ventral margin (vs. completely asquamate), a pointed and mildly convex predorsal profile (vs. blunt and strongly convex), and a second lacrimal plate that forms a part (albeit small) of the orbit margin (vs. second lacrimal plate excluded from orbit margin). The pigmentation pattern of *P.*

kieneri is conspicuously blotchy, mottled, and irregular, whereas *P. gymnopreopercularis* is characterized by a weakly mottled and essentially uniform chain-link lateral pigmentation pattern, owing to darkly pigmented scale margins.

DESCRIPTION: Morphometric and meristic data presented in table 5. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 36–37. A shallow bodied and comparatively small *Paretroplus* belonging to Clade H (fig. 1) that rarely exceeds 150 mm SL (e.g., largest wild caught specimens examined, from Mahajamba River and referred to as "géant" measured 160.0 mm SL). Head moderately pointed and snout curved (= convex), lending a beaked appearance to the species. Predorsal profile moderately (Lac Kinkony population) to strongly (Mahajamba River population) curved. Dorsal body outline slightly curved, ventral outline mostly straight, except posteriorly. Caudal peduncle short, moderately deep, and laterally compressed. No sexually dimorphic characters apparent.

Total vertebral count 32 or 33 (mode 32), with formulae of: 15 + 17, 15 + 18, 16 + 16, and 16 + 17 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, and other teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw number four to seven on each side, and total 8–13. Teeth in lower jaw number four to six on each side, and total 8–11. Upper- and lower-jaw teeth widely set, except for central (i.e., symphyseal and adjacent) teeth in the lower jaw, which are closely set.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. LPJ well sutured, with numerous interdigitating sutures on posteroventral margin. Six or seven robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. In some specimens, tooth plates on fourth ceratobranchial bones become fused. Tooth plates not confluent with outer-row (= lateral) gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three to four rows.

Nine or 10 (mode 9) triangular, somewhat elongate, gill rakers arrayed along lower limb of first gill arch. Rakers weakly to moderately denticulate dorsomedially in larger individuals. All other lower-limb rakers (i.e., those on gill arches 2–4) short, strongly denticulate dorsally, and spherical in shape. Teeth on rakers of gill arches 2–4 as long or longer than raker itself. Epibranchial rakers on first gill arch elongate, numbering seven or eight.

Body covered with large, regularly imbricate, cycloid scales. Well-developed scale ridges (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from spiny dorsal and anal fins, but becoming weakly attached to both soft dorsal and anal. Pelvic axillary scale present and well developed. Lateral-line scales number 33–40 (mode 38). Chest scales only slightly smaller than lateral body scales and somewhat embedded. Belly scales along ventral midline markedly reduced in size and much smaller than lateral body and chest scales. Four to six rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Preopercle fully scaled except ventrally and along extreme posterior margin of shaft. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly 2/3 to over 3/4 length of fin on dorsal and ventral lobes, and about 1/4 to 1/3 length of fin medially.

Dorsal with XVIII–XX spines, 13–15 soft rays. Anal with IX–XI spines, 11 or 12 soft rays. Origin of dorsal fin at about level of, or slightly posterior to, a vertical through pectoral-fin insertion. Caudal fin emarginate, trailing margins of upper and lower lobes slightly produced in larger individuals. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins weakly produced and pointed in larger specimens. Distal margins of soft dorsal and anal fins extend well past caudal-fin origin, even in smaller individuals. Pelvic fins extending just past anal-fin origin when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital excavations present. Paired anterior gas bladder bullae with tough and thickened tunica externa, and anteriormost chambers firmly lodged in exoccipital recesses. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

Coloration in Life: Base body coloration ranges from a blotchy, mottled, and speckled yellowish orange, grey, and olive, to a speckled dark brown (usually a combination of these colors are present) (see de Rham and Nourissat, 2004: 112, for color photographs). The Malagasy name for this fish, *kotsovato*, refers to its resemblance to the coloration of rocks (= *vato* in Malagasy). Coloration varies depending on drainage basin. Body pigmentation generally darker dorsally, but sometimes nearly uniformly pigmented. Head region and fins frequently gray, dark gray, or mottled dark brown and gray. No vertical bars present, even in juvenile specimens. Juveniles mottled golden and brown, and appearing camouflaged (under about 75 mm SL). Mottling in juveniles is in the form of large wavy blotches, as compared to much finer mottling and speckling in adults.

Coloration in Preservative: Body ground coloration ranges from a blotchy, mottled, and speckled pale yellow, to golden brown or grayish brown (figs. 36–37). As for live specimens, coloration varies depending on drainage basin from which the specimen was collected. Body pigmentation generally darker dorsally. Fin coloration olive, light gray, or uniform dark gray. Portions of head and dorsal flanks frequently dark gray or dark grayish brown (e.g., fig. 37). No other distinctive markings present. Juveniles mottled golden and brown, and appearing camouflaged (and similar in pigmentation pattern to juvenile *P. gymnopreopercularis*) due to presence of much larger and more well-defined blotches as compared to adults.

Distribution and Habitats: *Paretroplus kieneri* exhibits a relatively widespread distribution in northwestern Madagascar, and it occurs in both rivers and the shallow and turbid floodplain lakes characteristic of this region (fig. 38). The species' range from southwest to northeast includes the Mahavavy du Sud basin and Lake Kinkony (where it is presumed extinct), the lower Betsiboka basin, including Lake Ravelobe, the Akalimilotrabe (= Kalamilotra) River, Lake Parinandrina (see below), the Ikopa basin lakes, the upper Kamoro River, the Mahajamba River, and the Bemarivo basin and Lake Sarodrano, which are within the Sofia River drainage system (de Rham and Nourissat, 2004). To the north and northeast of the Bemarivo drainage basin, *P. kieneri* is replaced by *P. gymnopreopercularis*, which appears to be endemic to the Amboaboa-Mangarahara river system, a tributary of the extensive Sofia River drainage basin (fig. 38). No members of *Paretroplus* are known to occur to the southwest of the Mahavavy du Sud drainage system.

While in Madagascar in late 2003, I received a single dried specimen from J.-C. Nourissat that he labeled, "*Paretroplus* new species, Lac Amparimenidrino". I did not know at the time that this specimen was referred to as the "Red Damba" from Lake Parinandrina, which de Rham and Nourissat (2004: 129–130) hypothesized may represent a new species. We immediately obtained DNA-sequence data for this dried specimen,

and included it in a family-level phylogenetic study of cichlid fishes, in which this individual was robustly recovered as a member of a clade comprising several populations of *P. kieneri* (Sparks and Smith, 2004: fig. 1). It is interesting to note that de Rham, having only seen a picture of this fish, thought that it could be an emaciated *P. kieneri* (de Rham and Nourissat, 2004: 130), a result we have been able to corroborate using nucleotide characters.

Although *P. kieneri* is comparatively widespread in distribution for species of *Paretroplus*, which generally exhibit remarkably restricted (allopatric) distributions, I have found it to be nowhere abundant, or even common for that matter. Interestingly, throughout much of its range, specimens we have collected over the past decade generally appear to be in poor physical condition, being both emaciated and heavily infested with parasites. De Rham and Nourissat (2004) report that the Lake Kinkony (topotypic) population of *P. kieneri* is extinct, with no specimens collected since the mid-1990s (I last collected a few specimens from Lake Kinkony in 1994). At that time, *P. dambabe* was still relatively common in Lake Kinkony (now also presumed extinct in the basin), although our team encountered only four specimens of *P. kieneri* in several full days of fishing. Fortunately, de Rham and Nourissat (2004) report that *P. kieneri* is still abundant in some habitats, and although they do not specify which populations, one can assume they are referring to the recently discovered upper Kamoro and Mahajamba river populations (both of which have been included in this study).

LOCAL NAMES: *Kotsovato*.

ETYMOLOGY: Named after A. Kiener, a French fisheries researcher who conducted numerous studies in Madagascar in the 1950s and 1960s, and who is credited with obtaining the type series.

RELATIONSHIPS AND DISCUSSION: Based on the simultaneous analysis of morphological features and nucleotide characters, *P. kieneri* is recovered as a member of Clade H and as the sister taxon to *P. gymnopreopercularis* (fig. 1). Clade H is supported by a single unambiguously optimized unique and unreversed morphological feature, the presence of a blotchy, mottled, and speckled overall pigmentation pattern (figs. 36–37). This clade in turn is recovered as the sister taxon to Clade I, which comprises all deep-bodied members of the genus (i.e., *P. polyactis*, *P. maculatus*, *P. dambabe*, *P. petiti*, *P. menarambo*, and *P. maromandia*) (fig. 1). Prior studies based only on the analysis of nucleotide characters (Sparks, 2004a; Sparks and Smith, 2004) recovered a clade comprising *P. kieneri* and *P. gymnopreopercularis* as the sister taxon to a clade comprising the deep-bodied members of *Paretroplus* (Sparks and Smith, 2004: fig. 1), less *P. polyactis*. In these molecular phylogenetic studies, *P. polyactis* was recovered as the sister taxon to a clade comprising *P. kieneri* + *P. gymnopreopercularis* and the deep-bodied members of *Paretroplus* restricted to western basins (here Clade J).

Noting slight differences in body shape, coloration, and pigmentation pattern among the various populations spanning several drainage systems in northwestern Madagascar, some researchers have suggested that *P. kieneri* may represent a complex of species (e.g., de Rham and Nourissat, 2004). A recent molecular phylogenetic study, using both mitochondrial and nuclear nucleotide characters and which included representatives from four geographically distinct populations of *P. kieneri* distributed throughout northwestern Madagascar, was unable to resolve their intrarelationships (Sparks and Smith, 2004: fig. 1). Results of another, less comprehensively sampled, recent phylogenetic study (Sparks, 2004a) also based on nucleotide characters provided evidence for the existence of two species within this clade, *P. kieneri* and a closely related and previously undescribed taxon from the Amboaboa-Mangarahara River system, *P. gymnopreopercularis*, which is formally described in the current publication.

The phylogenetic analysis presented herein and based on the simultaneous analysis of morphological features and nucleotide characters further corroborates the hypothesis that *P. kieneri* and *P. gymnopreopercularis* are distinct species (fig. 1). Although the Amboaboa–Mangarahara River population, *P. gymnopreopercularis*, could be diagnosed on the basis of a single apomorphic morpho-

logical feature, none of the other populations spanning the range of *P. kieneri* could be distinguished from topotypical *P. kieneri* by unique (= apomorphic) morphological features. It is important to note that in the aforementioned molecular phylogenetic studies, the Bemarivo River (Lake Sarodrano) population could not be included due to lack of a tissue sample suitable for molecular studies. The Bemarivo River, like the Amboaboa-Mangarahara drainage to which *P. gymnopreopercularis* is endemic, is a tributary of the extensive Sofia River drainage basin. Although members of these two populations from within the Sofia River basin could be distinguished by squamation of the preopercle, it would be informative to see whether nucleotide characters also support this distinction. In conclusion, until the interrelationships of these populations can be sorted out, assuming they can be via either the use of additional, more quickly evolving nucleotide sequences or apomorphic morphological features, I believe that it is prudent to consider *P. kieneri* to represent a single, widespread species that spans several drainage basins in northwestern Madagascar.

In addition to differences in body shape (e.g., the body is noticeably deeper in the Lake Ravelobe individuals compared to all other populations examined), pigmentation pattern, and coloration among the various populations currently referred to *P. kieneri*, the degree of squamation on the preopercle is also to some extent variable among (and even within) the various geographic populations. Regardless, there is a distinct difference between the completely asquamate condition in *P. gymnopreopercularis* and all populations of *P. kieneri*, in which the preopercle is asquamate only along its ventral margin (e.g., in the Lake Kinkony and Lake Ravelobe populations). Both *P. kieneri* and *P. gymnopreopercularis* are characterized by a fleshy snout that extends rostrally anterior of the lips and also ventrally to slightly cover a portion of the upper lip.

Apart from degree of squamation on the preopercle (scaled in *P. kieneri* vs. asquamate in *P. gymnopreopercularis*), other useful (but not diagnostic) features for distinguishing *P. kieneri* and *P. gymnopreopercularis* are overall coloration and shape of the caudal peduncle. *Paretroplus kieneri* generally exhibits dark gray coloration somewhere on the body (frequently on the head), whereas *P. gymnopreopercularis* is never dark gray, but orangish to yellow overall. The caudal peduncle in *P. kieneri* is notably shorter and deeper than in *P. gymnopreopercularis* (caudal peduncle length/depth 0.4%–0.6%SL [mean 0.5] in *P. kieneri* vs. 0.5%–0.8%SL [mean 0.7] in *P. gymnopreopercularis*).

Paretroplus maculatus Kiener and Maugé, 1966

Figures 35, 39–41; plate 1E; table 6

Paretroplus damii: Kiener, 1963 (in part): Pl. 15, illustration 2: Specimen is an amalgam of *P. damii* (body) and *P. maculatus* (only member of genus with large black lateral blotch).

Paretroplus cf. *maculatus* Lake Marajory: de Rham and Nourissat, 2004: 101–102, including photograph.

SYNTYPES: MNHN 1965-315, 2 ex., 88.6–124.5 mm SL; northwestern Madagascar: Province of Majunga: Ambato-Boeny (Ambatoboemy [sic] in MNHN database); Kiener and Maugé, IX-1964.

NOTES ON TYPE LOCALITY: In the original description of *P. maculatus*, Kiener and Maugé (1966: 69–70) state "cette espèce, originaire du nord-ouest de Madagascar, est couramment capturée dans la zone du lac Amparihibe-Sud, Tsaramandroso, and Kamoro"; however, no specific type locality was provided for the two syntypes described. In the MNHN database, Ambato-Boeny ("Ambatoboemy" [sic]) is listed as the collection locality. This most likely was because Ambato-Boeny is the nearest town of substantial size somewhat centrally located within this region of occurrence. Regardless, the specific basin in which the two syntypes were collected remains unknown.

ADDITIONAL MATERIAL EXAMINED: AMNH 97362, 1 ex., 114.3 mm SL; northwestern Madagascar: Mahajanga Province: Lake Ravelobe: Station Forestiere d'Ampijoroa; P. V. Loiselle, R. Morris, and station staff, 25-VI-1993. AMNH 238559, 2 ex., 117.0–128.5 mm SL; northwestern Madagascar: Province of Mahajanga: Betsiboka drainage basin: near Ambato-Boeny: Lake Marajory; JSS 31-2003; J. Andriamianami-

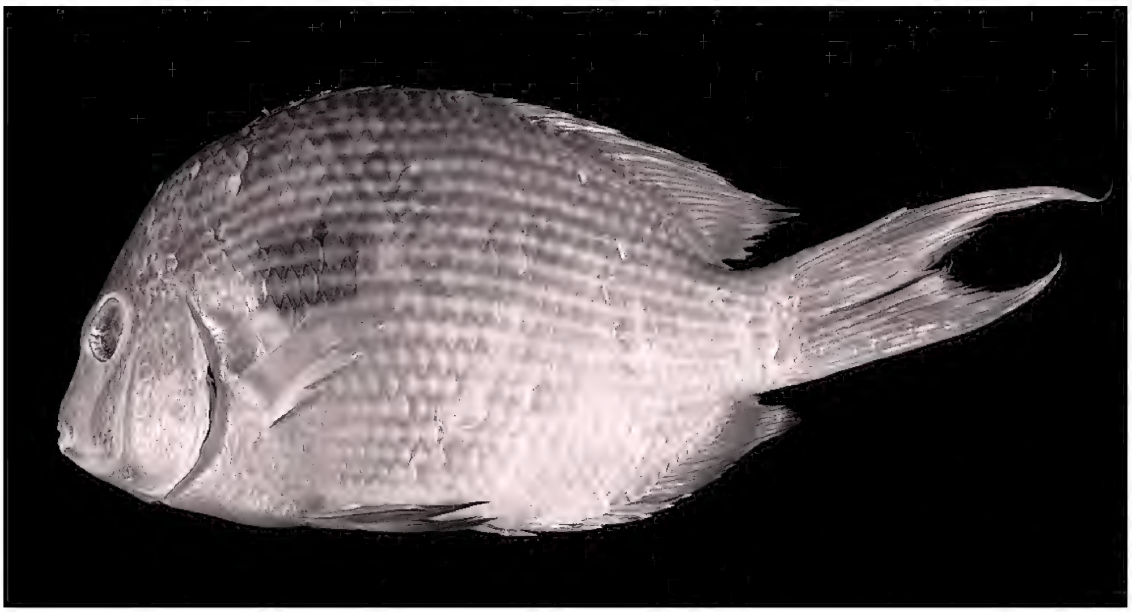


Fig. 39. *Paretroplus maculatus,* syntype, MNHN 1965-315, 124.5 mm SL; northwestern Madagascar: Mahajanga (= Majunga) Province: Ambato-Boeny (regions of Amparihibe-Sud, Tsaramandroso, and Kamoro). Note: image reversed and right side shown due to distortion of specimen.

Fig. 40. *Paretroplus maculatus*, MHNG 2537.47, adult, 141.7 mm SL, northwestern Madagascar: Mahajanga (= Majunga) Province: Ampijoroa Forestry Station: Lake Ravelobe. Nontype specimen illustrating pigmentation pattern of material collected more recently than type series.

Fig. 41. *Paretroplus maculatus*, UMMZ 235020, juvenile, 47.3 mm SL, illustrating individual in process of losing characteristic juvenile mottling and developing large humeral blotch and lateral banding pattern characteristic of adults.

haja and J.-C. Nourissat, X-2003 to XI-2003. AMNH 238568, 2 ex., 106.3–112.7 mm SL; northwestern Madagascar: Province of Mahajanga: Betsiboka drainage basin: near Ambato-Boeny: Lake Marajory; JSS 43-2003; J. Andriamianamihaja and J.-C. Nourissat, 2002. MHNG 2537.47, 6 ex., 1 ex. C&S, 90.1–143.2 mm SL; northwestern Madagascar: Province of Mahajanga: Ampijoroa Forestry Station: Lake Ravelobe; P. de Rham and J.-C. Nourissat, 24-X-1992. UMMZ 235019, 31 ex., 2 ex. C&S, 2 ex. S, 68–149 mm SL; northwestern Madagascar: near Ampijoroa Forestry Station: Lac Ravelobe: 16°18′31.0″S, 46°48′59.0″E; JSS 96-24; J. S. Sparks and K. J. Riseng, 14-VIII-1996. UMMZ 235020, 31 ex., 2 ex. C&S, 48.4–145.0 mm SL; northwestern Madagascar: Province of Mahajanga: across highway from Ampijoroa Forestry Station: Lac Ravelobe: 16°18′34.0″S, 46°48′59.0″E; JSS 94-10; J. S. Sparks and K. J. Riseng, VII-1994. UMMZ 240354, 1 ex. S, 85 mm SL; northwestern Madagascar: Lake Ravelobe; Laif Demason, 1995. UMMZ 240364, 1 ex. S, 76 mm SL; northwestern Madagascar: Lake Ravelobe; J. S. Sparks and K. J. Riseng. UMMZ 242081, 3 ex. S, 58–70 mm SL; northwestern Madagascar: near Ampijoroa Forestry Station: Lake Ravelobe; J. S. Sparks and K. J. Riseng, from aquarium shipment, 1996.

DIAGNOSIS: A member of the deep-bodied clade of *Paretroplus* (Clade I) and distinguished from all congeners by the presence of a large and essentially square to rounded solid black pectoral (= humeral) patch, located above and slightly posterior to the pectoral-fin base, and generally not extending dorsal to the upper branch of the lateral line.

DESCRIPTION: Morphometric and meristic data presented in table 6. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 24B and 39–41. A deep-bodied, laterally compressed *Paretroplus* belonging to Clade I, which comprises all deep-bodied and essentially disk-shaped members of *Paretroplus* (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, *P. petiti*, and *P. polyactis*) (fig. 1). Head blunt and steeply sloping in lateral view. Predorsal profile rounded and markedly convex, particularly in larger individuals. Caudal peduncle short, deep, and laterally compressed. Apart from unpaired fins of males slightly more elongate

TABLE 6
Morphometric and meristic data for *Paretroplus maculatus*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (S) indicates counts corresponding to syntypes (n = 2).

	P. maculatus					
		Syntypes				
Character	N	(1)	(2)	Range	Mean	SD
Standard length (mm)	20	88.6	124.5	48.4–148.1	106.5	
Percentage of SL						
Head width (max.)	20	15.8	16.3	15.8–17.5	16.7	0.38
Head length	20	32.1	30.4	28.4–32.4	29.8	1.01
Body depth	20	54.7	55.9	51.2–60.5	56.6	2.32
Caudal peduncle length	20	7.1	7.7	5.2–7.7	6.4	0.58
Caudal peduncle width	20	4.3	4.8	3.6–4.8	4.1	0.33
Caudal peduncle depth	20	14.6	15.7	14.6–16.6	15.8	0.50
Pectoral-fin length	20	25.1	23.1	20.9–25.1	22.4	1.17
Pelvic-fin length	20	24.2	24.7	22.7–25.1	24.0	0.68
Last dorsal spine length	18	N.A.	N.A.	12.9–18.2	16.6	1.13
Percentage of HL						
Snout length	20	37.7	46.3	36.9–47.0	42.9	2.64
Orbit diameter	20	36.6	31.2	30.3–37.6	33.7	1.77
Upper jaw length	20	26.4	27.8	26.1–29.3	27.5	0.81
Lower jaw length	20	33.8	32.3	32.1–36.6	34.4	1.11
Interorbital width	20	31.3	35.2	31.3–40.0	36.9	2.28
Preorbital depth	20	28.2	31.5	27.4–34.7	31.5	1.93
Caudal peduncle length/width	20	1.7	1.6	1.3–1.9	1.6	0.16
Caudal peduncle length/depth	20	0.5	0.5	0.3–0.5	0.4	0.04
Scales in lateral line	20	34 (1), 35 (1), 36 (4) (S2), 37 (4), 38 (8) (S1), 39 (2)				
Scales: lateral line to dorsal fin	20	6 (1) (S1), 6.5 (1), 7 (18) (S2)				
Gill rakers (lower limb 1st arch)	20	9 (1) (S2), 10 (17) (S1), 11 (2)				
Vertebrae (precaudal + caudal)	33	14 + 18 = 32 (12) (S1), 14 + 19 = 33 (14), 15 + 18 = 33 (7) (S2)				
Dorsal fin	33	XV 19 (1), XV 20 (2) (S1), XVI 16 (1), XVI 18 (3) (S2), XVI 19 (10), XVI 20 (4), XVII 17 (2), XVII 18 (6), XVII 19 (2), XVII 20 (1), XVIII 18 (1)				
Anal fin	33	VIII 15 (4), VIII 16 (2) (S2), IX 13 (2), IX 14 (5), IX 15 (15) (S1), IX 16 (3), X 15 (2)				

and pointed distally than females of comparative standard length, no additional sexually dimorphic features readily apparent.

Total vertebral count 32 or 33 (mode 33), with formulae of: 14 + 18, 14 + 19, and 15 + 18 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, and other teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw usually number six to eight on each side, and total 13–14. Teeth in lower jaw number five or six on each side, and total 10–11. Upper-jaw teeth widely set and evenly spaced, lower-jaw teeth widely set and irregularly spaced.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fused fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. LPJ well sutured, with numerous

interdigitating sutures on posteroventral margin. Seven robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Tooth plates not confluent with outer-row (= lateral) gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three or four rows.

Nine to 11 (mode 10) elongate triangular gill rakers arrayed along lower limb of first gill arch. Ceratobranchial rakers on first gill arch edentate in smaller specimens, becoming denticulate dorsomedially in larger individuals. All other lower-limb rakers (i.e., those on gill arches 2–4) short, stout, and strongly denticulate dorsally. Epibranchial rakers on first gill arch somewhat elongate and number 10 or 11.

Body covered with large, regularly imbricate, cycloid scales. Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from both spiny and soft portions of dorsal and anal fins. Pelvic axillary scale present and well developed. Interpelvic scale elongate and pointed. Lateral-line scales number 34–39 (mode 38). Chest scales only slightly smaller than lateral body scales and weakly embedded. Belly scales along ventral midline markedly reduced in size and embedded, much smaller than lateral body and chest scales. Five or 6 rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Preopercle ranges from asquamate only ventrally and along posterior margin of shaft to more or less completely asquamate. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly 2/3 to 3/4 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XV–XVIII spines, 16–20 soft rays. Anal with VIII–X spines, 13–16 soft rays. Origin of dorsal fin slightly anterior of vertical through pectoral-fin insertion. Caudal fin deep-bodied, strongly emarginate and crescent shaped, trailing margins of upper and lower lobes produced, particularly in larger individuals. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins produced and pointed in larger specimens, particularly males. Pelvic fins extending slightly beyond anal-fin origin when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital excavations present. Paired anterior gas bladder bullae with tough, thickened tunica externa and narrow tubular connections (= diverticula) to main gas bladder chamber. Anteriormost chambers firmly lodged in exoccipital recesses. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977) and nearly to anterior margin of frontals (fig. 6C). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

Coloration in Life: Conspicuous alternating light (pale golden brown, yellowy green, or grayish green) and dark (dark olive to dark reddish brown) horizontal stripes present on flanks (de Rham and Nourissat, 2004: 90–91). Presence of large, essentially square to rounded, solid black pectoral (= humeral) patch, usually four scale rows deep, located above and slightly posterior to pectoral-fin base. Black patch generally not extending dorsal to upper branch of lateral line (but see photograph in de Rham and Nourissat, 2004: 91). Flanks usually somewhat darker dorsally, but frequently uniform. Six or seven (bar on caudal peduncle is very faint to essentially lacking in larger specimens) broad, vertical, dark olive bars on flanks, extending from anterior region of trunk to caudal peduncle. Bars more prominent dorsally and midlaterally on flank, yet always faint; bars very obvious in juveniles, becoming less conspicuous and barely discernable in large adults. Patch of red spots on flanks reported in some specimens (de Rham

and Nourissat, 2004: 89–90). Nape, postorbital region, and region below anterior spinous dorsal ranges from grayish brown to reddish. Opercular region and cheek golden brown, golden green, or reddish. Black interorbital bar present in adults. Interorbital region grayish to pale golden brown anterior to black bar. Gular region ranges from light gray or grayish blue to blackish. Ventral chest and belly grayish brown to black. Dorsal and anal fins olive or gray proximal to base, and reddish distally. Caudal fin charcoal anteriorly and medially, and reddish distally. Spines of dorsal fin red distally. Soft dorsal and anal fins, and caudal fin with vivid red terminal band. Pectoral fins dark gray to black. Pigmentation pattern of young fish (to about 30 mm SL) characterized by large golden-brown blotches and mottling, such that fish appears camouflaged (e.g., see juvenile *P. petiti* [now *P. dambabe*] illustrated by Kiener [1963: Pl. 16], which exhibits a similar pigmentation pattern).

Coloration in Preservative: Similar to live coloration, except that reddish coloration on flanks, head, and fins is more or less lost in preservative. Conspicuous alternating light (pale golden brown or light olive) and dark (dark olive, dark grayish brown, or dark brown) horizontal stripes present on flanks. Large, more or less square to rounded, black pectoral (= humeral) patch, present on anterior flank, above and slightly posterior to pectoral-fin base (figs. 24B and 39–41). Six or seven broad and faint dark olive bars on flanks; bars more conspicuous in juveniles and smaller individuals. Interorbital region, lacrimal, and snout grayish. Lips golden-brown to grayish. Gular region, anterior chest, belly, interopercle, and ventral cheek dark brown to black. Pelvic fins black. Pectoral fins pale golden-brown to olive. Unpaired fins golden brown, brownish gray, or near uniform dark gray. Anal fin with black terminal band; sometimes anal fin almost uniform black. Dorsal fin usually with weak black terminal band. Base of caudal fin golden to dark grayish-brown. Young fish (to about 30 mm SL) characterized by large golden-brown blotches and mottling, such that fish appears camouflaged.

Viscera and Diet: Gut contents comprised entirely of macerated gastropods in all individuals examined. *Paretroplus maculatus* appears to feed exclusively on gastropods.

Distribution and Habitats: *Paretroplus maculatus* is endemic to turbid, shallow floodplain lakes in the lower reaches of the Betsiboka and Ikopa drainage basins in northwestern Madagascar (fig. 35). The range of *P. maculatus* extends in the north from Lake Ravelobe and surrounding small rivers in the vicinity of Ampijoroa Forestry Station, located to the southeast of Mahajunga (= Majunga), southward to a number of small lakes in the vicinity of Maevatanana (de Rham and Nourissat, 2002, 2004), including lakes in the region of Ambato-Boeni (Kiener and Maugé, 1966: "dans la zone du lac Amparihibe-Sud, Tsaramandroso, and Kamoro"; de Rham and Nourissat, 2004), which is more or less centrally located between Ampijoroa and Maevatanana. Lake Andimaka, located to the southwest of the town of Mahazoma, which itself is located to the southwest of Maevatanana, is the most southerly collection locality known for *P. maculatus*. De Rham and Nourissat (2004) hypothesize that the rapids of the middle courses of the Betsiboka and Ikopa rivers act as barriers to the upstream dispersal of *P. maculatus*, restricting it to the lakes (and small rivers, personal obs.) of the lower reaches of these drainage basins.

Based on collections I have made and those of colleagues spanning several years, *P. maculatus* appears to have suffered a severe decline in abundance in recent years throughout its range. Severe fishing pressure, habitat degradation, and the introduction of a number of exotic species, most notably the Asian snakehead, *Channa* sp., are probably the largest factors accounting for the rapid attrition of *P. maculatus*. Another member of *Paretroplus*, *P. kieneri*, is also found throughout the range of *P. maculatus*. This species has become increasingly rare in recent years according to local fishermen, and is considered to be extinct in its type locality, Lake Kinkony.

Local Name: *Damba*.

Etymology: The specific name *maculatus* (from the Latin *maculae*, meaning "spot")

refers to the large black humeral patch, which is diagnostic of this taxon.

Relationships and Discussion: *Paretroplus maculatus* is a member of Clade I, comprising all of the deep-bodied and essentially disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maromandia*, *P. menarambo*, *P. petiti*, and *P. polyactis*), which is supported by three unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1). Apart from pigmentation pattern and coloration, all members of this clade are morphologically very similar.

In the combined analysis of morphological features and nucleotide characters, *P. maculatus* is recovered in an unresolved polytomy with all other deep-bodied species of *Paretroplus* that have distributions restricted to western basins (fig. 1: Clade J). Monophyly of Clade J, comprising *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*, is supported by two unambiguously optimized morphological features, the second of which is unique and unreversed: the presence of a blunt snout with a steeply sloping profile in lateral view and a distinctive lateral pigmentation pattern comprising alternating horizontal light and dark stripes. A lack of resolution within Clade J is due to the fact the *P. petiti* (known only from the formalin-fixed holotype) is included on the basis of morphological features only, which are insufficient for resolving relationships within this morphologically conservative clade. In a combined analysis of morphological features and nucleotide characters that specifically excluded *P. petiti*, *P. maculatus* is recovered as the sister taxon to *P. dambabe* (fig. 2), a result also obtained on the basis of nucleotide characters only (Sparks, 2004a; Sparks and Smith, 2004).

In a paper describing a new species of *Paretroplus* from Lake Kinkony (Sparks, 2002a), I reported that *P. petiti* is currently known only from the holotype (MNHN 1928.282), a juvenile specimen. After communicating my findings regarding the status of *P. petiti* Pellegrin, 1929, which I consider to be very closely related to, and possibly conspecific with, the fish later described as *P. menarambo* Allgayer, 1996 (see Sparks, 2002), J.-C. Nourissat collected and provided me with specimens (AMNH 238559 and AMNH 238568) from Lake Marajory in the Betsiboka-Kamoro drainage basin, which were labeled *P.* cf. *maculatus*. These specimens exhibit the large black humeral patch diagnostic of *P. maculatus*. They are also reported to possess red spotting on the flanks (de Rham and Nourissat, 2004), a feature lacking in other populations of *P. maculatus*. De Rham and Nourissat (2004: 100–101) refer to these specimens as "*Paretroplus* sp. aff. *menarambo* Betsiboka-Kamoro" and discuss whether they may be referable to *P. petiti*. After examining the specimens, I disagree with this assessment, and consider the specimens to be clearly referable to *P. maculatus*, the only species with a black humeral blotch. (In an addendum to de Rham and Nourissat (2004) [dated August 2004], de Rham likewise considers these specimens to be conspecific with *P. maculatus*.) The holotype of *P. petiti* (MNHN 1928.282) is quite well preserved, particularly in terms of pigmentation pattern, and there is no trace of a humeral blotch (fig. 34). In the original description of *P. maculatus*, Kiener and Maugé (1966) list its range to include lake habitats in the regions of Amparihibe-Sud, Tsaramandroso, and Kamoro. The specimens in question from Lake Marajory were collected from within the Betsiboka-Kamoro drainage basin, and within the range attributed to this species in the original description.

Paretroplus menarambo Allgayer, 1996

Figures 35, 42–44; plate 1F; table 7

Holotype: MZUS (MZS) 3653, 128.2 mm SL; northwestern Madagascar: Mahajanga Province: Potamasina: Sofia River basin: Lake Sarodrano; J.-C. Nourissat and P. de Rham, 22-XI-1991. Not examined.

Paratypes: MZUS (MZS) 3654, 1 ex., 110.5 mm SL; data as for holotype; not examined. MNHN 1996-121, 1 ex., 89.4 mm SL; data as for holotype. MNHN 1996-122, 1 ex., 92.8 mm SL; data as for holotype.

Additional Material Examined: AMNH 97364, 2 ex., 1 ex. C&S, 79.8–124.0 mm SL; northwestern Madagascar:

Fig. 42. *Paretroplus menarambo*, paratype, MNHN 1996-122, 92.8 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River basin: Lake Sarodrano.

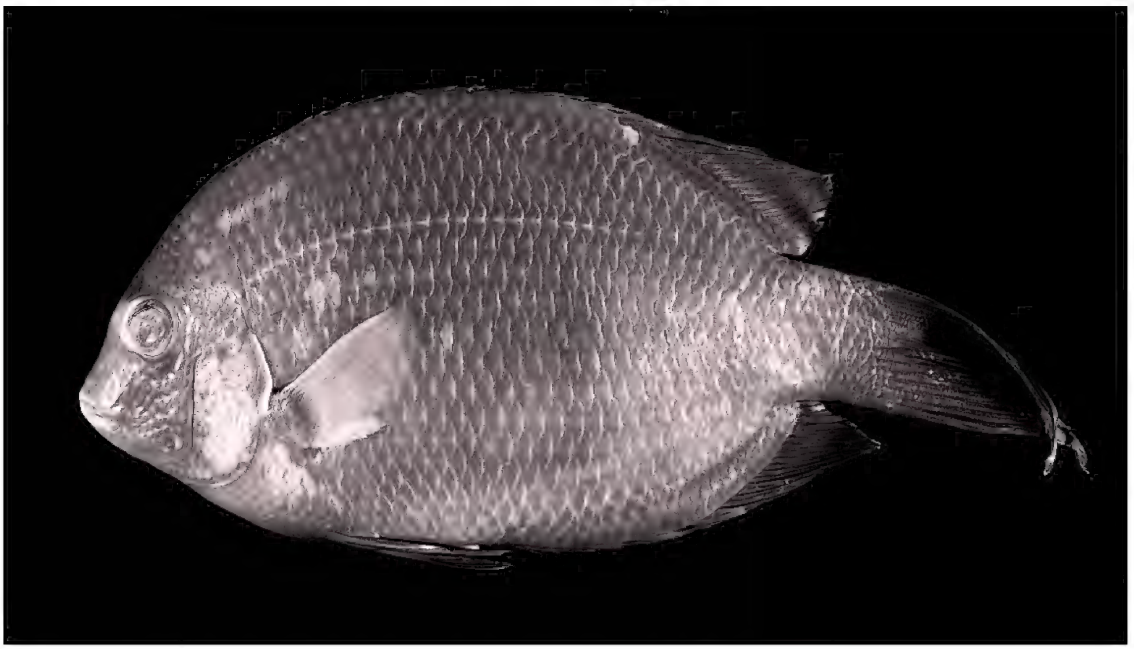


Fig. 43. *Paretroplus menarambo*, nontype specimen, UMMZ 235014, 163.5 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River basin: Lake Sarodrano. Illustrating pigmentation pattern of mature adult.

Fig. 44. *Paretroplus menarambo*, UMMZ 235014, 72.4 mm SL, illustrating more prominent lateral banding pattern characteristic of juveniles.

Mahajanga Province: Bemarivo River drainage (tributary of Sofia River): Lake Sarodrano; P. V. Loiselle and local fishermen, 23-VI-1993. AMNH 226311, 4 ex., 145–161 mm SL; aquarium trade specimens from stock collected in northwestern Madagascar: Mahajanga Province: Bemarivo River drainage (tributary of Sofia River): Lake Sarodrano. MHNG 2537.49, 4 ex., 95.0–185.4 mm SL; northwestern Madagascar: Mahajanga Province: Bemarivo River drainage: 30 km north of Mampinkony: Lake Sarodrano; P. de Rham and J.-C. Nourissat, 23-X-1992. UMMZ 233522, 6 ex., 1 ex. S, 148.0–160.00 mm SL; northwestern Madagascar: Mahajanga Province: Bemarivo River drainage: near village of Sarodrano, approx. 30 km north of town of Mampikony: Lake Sarodrano; aquarium specimens received from L. Demason, orig. collected by J. S. Sparks, K. J Riseng, and local fishermen. UMMZ 235013, 1 ex., 84.5 mm SL; northwestern Madagascar: Mahajanga Province: Bemarivo River drainage: near village of Sarodrano, approx. 30 km north of town of Mampikony: Lake Sarodrano: 15°47′46.0″S, 47°39′11.0″E; JSS 96-23; J. S. Sparks, K. J Riseng, and local fishermen, 18-VII-1996. UMMZ 235014, 28 ex., 2 ex. C&S, 72.0–167.0 mm SL; northwestern Madagascar: Mahajanga Province: Bemarivo River drainage: near village of Sarodrano, approx. 30 km north of town of Mampikony: Lake Sarodrano: 15°47′46.0″S, 47°39′10.0″E; JSS 94-16; J. S. Sparks, K. J Riseng, and local fishermen, 19-VII-1994.

DIAGNOSIS: A member of the deep-bodied clade of *Paretroplus* (Clade I) and distinguished from all congeners by the presence of a pinstriped lateral pigmentation pattern comprising numerous longitudinal series of prominent black spots on the flanks, owing to the presence of one large spot on each scale. *Paretroplus menarambo* is also unique among congeners in possessing a conspicuous black interorbital stripe and suborbital blotch.

DESCRIPTION: Morphometric and meristic data presented in table 7. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 21D and 42–44. A deep-bodied, laterally compressed *Paretroplus* belonging to Clade I, which comprises all deep-bodied and essentially disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. petiti*, and *P. polyactis*) (fig. 1). Head blunt and steeply sloping in lateral view. Predorsal profile

TABLE 7

Morphometric and meristic data for *Paretroplus menarambo*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (P1) indicates counts corresponding to MNHN 1996-121 and (P2) to MNHN 1996-122.

		P. menarambo				
		Paratypes				
Character	N	1996-121	1996-122	Range	Mean	SD
Standard length (mm)	20	89.4	92.8	72.1–166.8	121.9	
Percentage of SL						
Head width (max.)	20	16.2	15.6	14.9–17.2	16.0	0.61
Head length	20	31.1	31.5	28.0–31.5	29.3	0.85
Body depth	20	55.2	58.4	54.8–60.3	57.7	1.57
Caudal peduncle length	20	6.2	5.5	5.5–8.8	7.0	0.79
Caudal peduncle width	20	4.7	4.0	3.8–6.4	4.6	0.75
Caudal peduncle depth	20	15.8	15.3	15.0–17.4	16.3	0.69
Pectoral-fin length	20	24.3	24.0	20.7–24.3	22.0	0.95
Pelvic-fin length	20	22.4	23.8	22.4–25.2	23.8	0.76
Last dorsal spine length	18	N.A.	N.A.	14.2–17.6	15.9	1.08
Percentage of HL						
Snout length	20	38.5	40.4	38.5–47.9	43.8	2.68
Orbit diameter	20	32.0	32.2	27.3–32.5	30.8	1.32
Upper jaw length	20	26.3	26.7	26.3–29.4	27.7	0.88
Lower jaw length	20	34.9	32.2	32.2–36.4	34.4	1.01
Interorbital width	20	30.2	30.5	30.2–40.9	36.0	2.69
Preorbital depth	20	29.5	27.1	26.8–36.5	32.8	2.79
Caudal peduncle length/width	20	1.3	1.4	1.1–2.0	1.5	0.25
Caudal peduncle length/depth	20	0.4	0.4	0.4–0.5	0.4	0.05
Scales in lateral line	20	34 (1), 37 (14) (P1), 38 (5) (P2)				
Scales: lateral line to dorsal fin	20	6 (2) (P2), 6.5 (2) (P1), 7 (13), 7.5 (1), 8 (2)				
Gill rakers (lower limb 1st arch)	20	9 (18) (P1,2), 10 (2)				
Vertebrae (precaudal + caudal)	26	15 + 17 = 32 (1), 15 + 18 = 33 (23) (P1,2), 15 + 19 = 34 (1), 16 + 18 = 34 (1)				
Dorsal fin	26	XV 19 (2) (P2), XV 20 (4), XV 21 (5), XVI 19 (3), XVI 20 (9) (P1), XVI 21 (2), XVII 19 (1)				
Anal fin	26	VII 17 (1), VIII 15 (6) (P2), VIII 16 (10), IX 15 (9) (P1)				

rounded and convex, particularly in larger individuals. Caudal peduncle short, deep, and laterally compressed. No sexually dimorphic characters apparent, although unpaired fins of males slightly more elongate and pointed distally than females of comparative standard length.

Total vertebral count 32–34 (mode 33), with formulae of: 15 + 17, 15 + 18, 15 + 19, and 16 + 18 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws (fig. 3B). Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, other teeth graded in size laterally (fig. 5A). Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw number six to eight on each side, and total 14–15. Teeth in lower jaw number three to five on each side, and total 6–10. (Note: a single individual examined with three teeth on each side in lower jaw, otherwise four or five teeth on each side for a total of nine or 10.) Upper- and lower-jaw teeth widely set and more or less evenly spaced.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Denti-

tion on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. LPJ well sutured. Suture extensive with numerous finger-shaped interdigitating sutures on posteroventral margin. Five to seven robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Tooth plates not confluent with outer-row (= lateral) gill rakers of fourth ceratobranchial elements. Bases of some tooth plates becoming confluent, but majority separate. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three or four rows.

Nine or 10 (mode 9) elongate triangular gill rakers arrayed along lower limb of first gill arch. Rakers weakly denticulate dorsomedially. All other lower-limb rakers (i.e., those on gill arches 2–4) short, robust, more or less spherical in shape, and strongly denticulate dorsally. Teeth on rakers of gill arches 2–4 elongate, thin, conical, and curved near tip. Epibranchial rakers on first gill arch elongate and comparatively robust, numbering eight or nine.

Body covered with large, regularly imbricate, cycloid scales. Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases (fig. 22A). Scale ridges free from both spiny and soft portions of dorsal and anal fins. Pelvic axillary scale present and well developed. Terminal scale of interpelvic series robust, elongate, and rounded, or blunt and squared off distally. Lateral-line scales number 34–38 (mode 37). Chest scales only slightly smaller than lateral body scales and weakly embedded (fig. 23B). Belly scales quite small compared to other body scales and strongly embedded, those along ventral midline smallest. Six or seven rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Preopercle scaled except anteroventrally, and shaft fully scaled. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly 2/3 to well over 3/4 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XV–XVII spines, 19–21 soft rays. Anal with VII–IX spines, 15–17 soft rays. Origin of dorsal fin ranging from about level of, to slightly posterior of, vertical through pectoral-fin insertion. Caudal fin deep-bodied, strongly emarginate and crescent shaped, trailing margins of upper and lower lobes quite produced, particularly in larger individuals. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins produced and pointed in larger specimens. Pelvic fin extending just beyond anal-fin origin when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital foramina present (fig. 8B). Paired anterior gas bladder bullae with tough, thickened tunica externa and narrow tubular connections (= diverticula) to main gas bladder chamber. Anteriormost chambers firmly lodged in exoccipital recesses. Expansive, wide and rounded excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital (fig. 8B). Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae) (fig. 3B). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins. Modified "prezygopophyses" present on anterior neural arches (fig. 18B).

Coloration in Life: Body ground coloration ranging from light gray to iridescent grayish green. Prominent black spots on flanks arranged in numerous longitudinal series, and alternating with light gray to grayish-green stripes, lend fish a pinstriped appearance, hence its common name in the aquarist literature, *pinstripe damba* (see de Rham and Nourissat, 2004: 98–100). Series of six or seven (anteriormost bar[s] frequently

very faint in larger specimens) broad, vertical, dark charcoal to blackish bars on flanks, extending from anterior region of trunk to caudal peduncle. Lateral barring pattern very obvious in juveniles, becoming faint and less conspicuous, and frequently barely discernable, in large adults. Black interorbital stripe present as well as prominent black blotch on cheek below orbit. Head gray to iridescent grayish green, and generally somewhat darker dorsally. Snout and lacrimal gray. Unpaired fins gray, dark gray, or charcoal. Margins of dorsal, anal, and caudal fins vivid red, giving fish its Malagasy and scientific name *menarambo*, meaning "red tail" (see photos in de Rham and Nourissat, 2004: 100 and 133). Pectoral fins gray to grayish-green. Pelvic fins gray to charcoal. Breeding individuals exhibit intensification of dark vertical bars, but otherwise do not differ in coloration from sexually quiescent individuals.

Coloration in Preservative: Body ground coloration grayish brown to dark brown. *Paretroplus menarambo* notably darker in preservation than in life. Alternating dark (dark brown) and light (lighter brown) horizontal-striping pattern evident on flanks. Dark brown horizontal stripes due to presence of dark spots on scales arranged in numerous longitudinal series, lending fish a pinstriped pigmentation pattern (figs. 21D, and 42–43). Pinstriped flank pattern obvious, but much less pronounced than in live fish. Dark spotting on scales also much less prominent than in life. Head generally uniform dark brown. Subopercle and (to lesser degree) interopercle golden in some specimens, otherwise dark brown as on rest of head. Series of six or seven broad, vertical, dark charcoal to blackish bars on flanks, extending from anterior region of trunk to caudal peduncle. Lateral barring pattern very obvious in juveniles (to about 85 mm SL), becoming faint and frequently barely discernable in large adults. Juveniles lighter overall in coloration (golden brown, not dark brown) and with seven easily visible lateral bars, extending from caudal margin of opercle to caudal peduncle (fig. 44).

Distribution and Habitats: *Paretroplus menarambo* was until very recently considered extinct in the wild; no specimens had been collected since 1997 (de Rham and Nourissat, 2004). In mid-November of 2006, however, I received a message from Olaf Pronk in Madagascar stating that a friend of his (Jurgen Spannring) had collected what he considered to be *P. menarambo* from a single small lake about 30 km to the east of Port Bergé. Images of freshly caught specimens were included and the identity of *P. menarambo* could be easily confirmed. Prior to this, the species was only known from the type locality, Lake Sarodrano, although it was suspected that it might be present in similar floodplain lakes in the region, which remained poorly surveyed (fig. 35). Lake Sarodrano lies within the Bemarivo River floodplain between the towns of Mampinkony and Port Bergé in northwestern Madagascar. Lake Sarodrano is a typical floodplain lake characteristic of northwestern Madagascar. The lake is very shallow, extremely turbid, and lined and infested with large clumps of reeds. The Bemarivo River is a tributary of the extensive Sofia River drainage system, but the species is not reported from the Sofia. According to de Rham and Nourissat (2004: 99), who first discovered the species in November of 1991, local fishermen reported that *P. menarambo* once occurred in all of the Bemarivo River floodplain lakes, of which there are many, but that they had not collected specimens in recent years. Although *P. menarambo* apparently once occurred in lakes throughout the Bemarivo River drainage basin, up until November of 2006 the species had been collected by researchers only in Lake Sarodrano, locat ed just north of the town of Mampinkony. According to de Rham and Nourissat (2004), local fishermen confirmed the recent disappearance of *P. menarambo* from all of the Bemarivo floodplain lakes. Fortunately, the species still persists in similar habitats within the region, although it appears to have been extirpated from the type locality, Lake Sarodrano. In addition, colleagues and myself have exported specimens to the United States and Europe, where the species has done quite well in captivity and can now be obtained fairly easily from breeders.

LOCAL NAME: *Menarambo*.

ETYMOLOGY: The specific name *menarambo* is a compound Malagasy word that translates as *mena* (= "red") and *rambo* (= "tail") in reference to the vivid red caudal-fin margin of mature specimens.

RELATIONSHIPS AND DISCUSSION: *Paretroplus menarambo* is a member of Clade I, comprising all of the deep-bodied and more or less disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. petiti*, and *P. polyactis*), which is supported by three unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1). Apart from pigmentation pattern and coloration, all members of this clade are morphologically similar.

In the combined analysis of morphological features and nucleotide characters, *P. menarambo* is recovered in an unresolved polytomy with all other deep-bodied species of *Paretroplus* that have distributions restricted to western basins (fig. 1: Clade J). Monophyly of Clade J, comprising *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*, is supported by two unambiguously optimized morphological features, the second of which is unique and unreversed: the presence of a blunt snout with a steeply sloping profile in lateral view and a distinctive lateral pigmentation pattern comprising alternating light and dark horizontal stripes. A lack of resolution within Clade J is due to the fact the *P. petiti* (known only from the formalin-fixed holotype) is included on the basis of morphological features only, which are insufficient for resolving relationships within this anatomically conservative clade. In a combined analysis of morphological features and nucleotide characters that specifically excluded *P. petiti*, *P. menarambo* is recovered as the sister taxon to *P. maromandia* (fig. 2), a result also obtained by the analysis of nucleotide characters only (Sparks, 2004a; Sparks and Smith, 2004: fig. 1).

In addition to substantial differences in pigmentation pattern (pinstriped in *P. menarambo* vs. prominently laterally barred in *P. maromandia*) and coloration (see respective descriptions in life and preservative), *P. menarambo* is distinguished from *P. maromandia* by number of scales in the lateral line (34–38 in *P. menarambo* vs. 39–41 in *P. maromandia*), and generally by the number of gill rakers on the lower limb of the first arch (9 in *P. menarambo* [2 of 20 specimens had a count of 10] vs. 10 in *P. maromandia*). Moreover, in *P. menarambo* the caudal fin is considerably more lunate and concave, with elongate trailing dorsal and ventral filaments in large specimens.

Paretroplus menarambo and *P. maromandia* are the only species of *Paretroplus* with a dorsal-fin ray count that exceeds 20 (range of 19–21 in *P. menarambo* and 20–23 in *P. maromandia*). Only *P. maculatus* has a dorsal-fin ray count that reaches 20 (range 16–20).

As discussed by Sparks (2002a), the holotype and only known specimen of *P. petiti* (fig. 34) is very similar in overall body shape and pigmentation pattern (in preservative) to *P. menarambo* Allgayer, 1996 (figs. 21D, and 42–43), a species historically restricted to lakes of the Bemarivo River floodplain within the Sofia River drainage system in northwestern Madagascar, but not occurring in the Sofia River itself (fig. 35). Despite being collected in the 1920s, the holotype of *P. petiti* is remarkably well preserved, particularly in terms of pigmentation pattern and coloration. In preservative, both *P. petiti* and *P. menarambo* are dark brown in overall coloration, with a lateral pattern characterized by numerous, thin, alternating light and dark horizontal stripes (cf. figs. 34 and 42). In preservative, no additional distinctive lateral markings are present in either of these species. In life *P. menarambo* is characterized by both a pinstriped lateral pigmentation pattern and broad red terminal bands in the unpaired fins. This unique pinstriped pattern is still obvious in many preserved specimens, whereas others appear more or less solid brown or grayish brown. Coloration in life for *P. petiti* is not known, and comparisons to *P. menarambo* cannot be made.

Pellegrin (1929) commented on the horizontal striping pattern mentioned above, but he did not note the presence of a series of broad vertical bars on the flanks of *P. petiti*. Pellegrin (1929) similarly made no reference to any additional distinctive markings in *P.*

Fig. 45. *Paretroplus nourissati*, holotype, MNHN 1997-4172, 98.2 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Mangarahara River.

petiti. Although other members of the deep-bodied clade of *Paretroplus* restricted to western basins (Clade J) possess this conspicuous alternating light and dark horizontal striping pattern, no species other than *P. petiti* and *P. menarambo* are dark brown with no additional lateral markings. As mentioned above, the vertical barring pattern on the flanks of *P. menarambo* is generally rather faint and difficult to discern in preservative, particularly in large adults. Vertical bars, if present at all, are very faint in the holotype of *P. petiti*, and although not mentioned in the original description may have faded considerably over time in preservative.

Specimens now assigned to *P. dambabe* Sparks, 2002a were historically (since at least the early 1960s) referred to *P. petiti* (e.g., Kiener, 1963; Kiener and Thérézien, 1963; Kiener and Maugé, 1966). The type specimen of *P. petiti*, a juvenile of 82.8 mm SL, is much deeper bodied than any individual of *P. dambabe* of similar standard length, and is in fact deeper bodied than any individual of *P. dambabe* examined (57.9% in *P. petiti* vs. max. 57.1% SL in *P. dambabe* of nearly 200 mm SL). Members of *Paretroplus* generally become deeper bodied with increasing standard length. Nevertheless, the holotype of *P. petiti* is very similar in body depth to specimens of *P. menarambo* of similar standard length (Sparks, 2002a: fig. 8). Sparks (2002a) discussed the possibility that *P. petiti* and *P. menarambo* are conspecific, but cautioned that further study is needed, which depends on acquiring additional material from the region of the type locality of *P. petiti*, which itself remains uncertain (see Sparks, 2002a). This is a difficult region of northwestern Madagascar to access, and no additional specimens have been collected to date (also see discussions above for both *P. dambabe* and *P. maculatus*).

Paretroplus nourissati (Allgayer, 1998)
Figures 45–48; plate 1G; table 8

HOLOTYPE: MNHN 1997-4172, 98.2 mm SL; northwestern Madagascar: Sofia River drainage basin: near town of Mandritsara: Mangarahara River; J.-C. Nourissat, X-1996.

PARATYPES: MNHN 1997-4173, 4 ex., 84.1–96.6 mm SL; data as for holotype.

ADDITIONAL MATERIAL EXAMINED: AMNH 229554, 2 ex., 1 ex. C&S, 87.0–106.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River: 15°50′1.0″S, 48°42′52.0″E; JSS 94-18; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 24-VII-1994. AMNH 229555, 3 ex., 1 ex. C&S, 72.0–78.0 mm SL; northwestern Madagascar: Mahajanga Prov-

Fig. 46. *Paretroplus nourissati*, UMMZ 235206, 116.3 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River.

ince: Sofia River drainage basin: near town of Mandritsara: Amboaboa River: 15°50′1.0″S, 48°42′51.0″E; JSS 96-25: altitude 210.3 m a.s.l.; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 10 and 11-VII-1996. AMNH 229562, 1 ex., 64.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: west of Mandritsara: Amboaboa River; PVL-93-VI-22; P. V. Loiselle, R. Morris, B. Vesta, and local villagers, 22-VI-1993. AMNH 236158, 4 ex., 40.8–107.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: Amboaboa River at Andrahamamy village; PVL-04-09; P. V. Loiselle. UMMZ 235205, 76 ex., 4 ex. C&S, 1 ex. S; 49.0–124.0 mm SL; data as for AMNH 229555. UMMZ 235206, 40 ex., 3 ex. C&S,

Fig. 47. *Paretroplus nourissati*, AMNH 236158, 40.4 mm SL, illustrating prominent lateral banding pattern in juveniles.

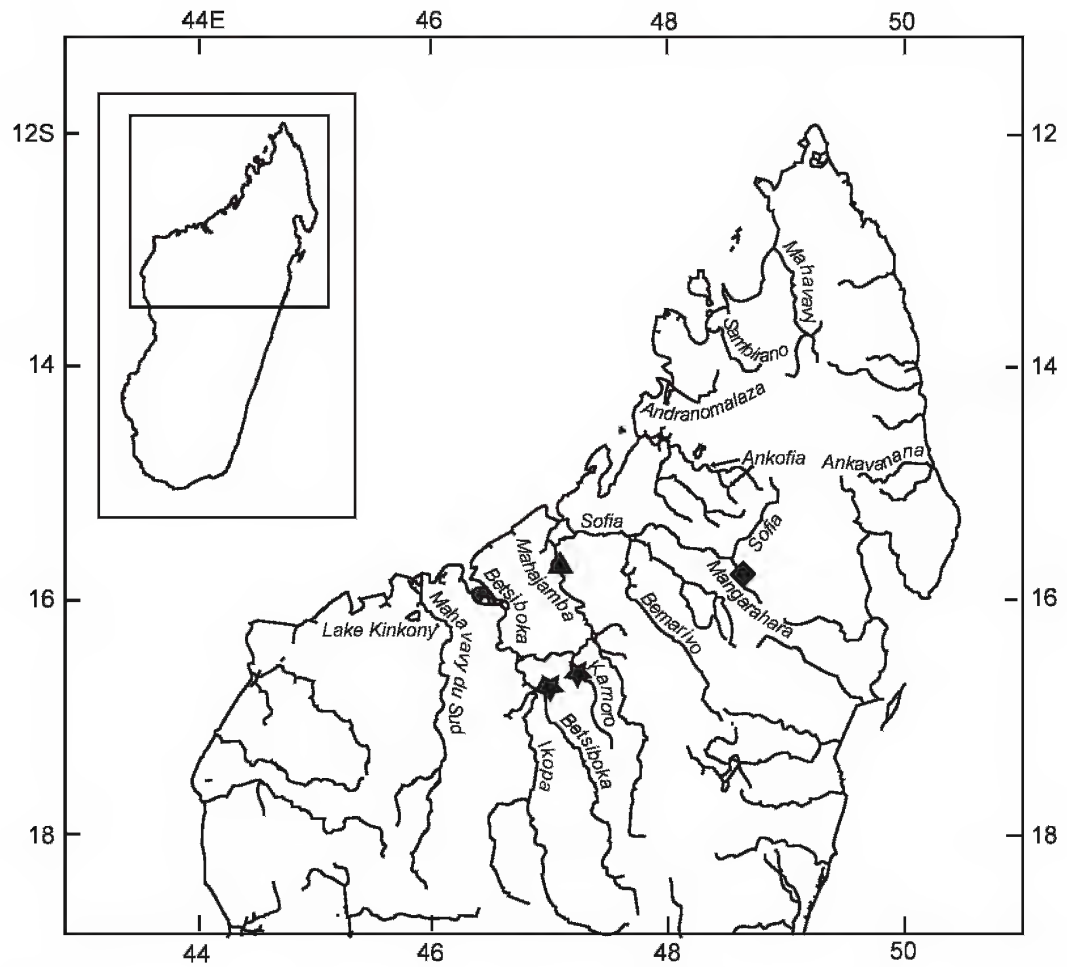


Fig. 48. Drainage map of northern Madagascar illustrating the known geographic ranges for members of Clade F, *Paretroplus nourissati* (diamond), *P. tsimoly* (stars), and *P. lamenabe* (triangle).

7.0–160.0 mm SL; data as for AMNH 229554. UMMZ 239530, 6 ex., 76.0–127.0 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: Mangarahara River just downstream from confluence with Amboaboa River, 15°50′1.0″S, 48°42′51.0″E: altitude 210.3 m a.s.l.; JSS 96-26; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 11-VIII-1996. UMMZ 239545, 3 ex., 76.0–90.0 m SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River: 15°50′2.0″S, 48°42′52.0″E; JSS 94-53; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 14-XI-1994. UMMZ 240363, 1 ex. S, 62.5 mm SL; northwestern Madagascar: Mahajanga Province: Sofia River drainage basin: near town of Mandritsara: Amboaboa River near confluence with Mangarahara River; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 10 and 11-VII-1996. UMMZ 243679, 1 ex. S, 70.7 mm SL; data as for UMMZ 240363.

DIAGNOSIS: A shallow-bodied, elongate *Paretroplus* diagnosed from all congeners except *P. lamenabe* and *P. tsimoly* by the presence of two wide and convergent (below the lateral midline) dark brown to black midlateral bands, representing the second and third or third and four bars in series. *Paretroplus nourissati* is diagnosed in life by a pigmentation pattern of broad vertical black

TABLE 8

Morphometric and meristic data for *Paretroplus nourissati*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

		P. nourissati			
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	20	98.2	55.9–158.2	95.8	
Percentage of SL					
Head width (max.)	20	16.0	15.9–18.3	17.3	0.62
Head length	20	35.2	31.6–36.9	34.7	1.15
Body depth	20	41.0	38.1–43.5	40.7	1.60
Caudal peduncle length	20	11.0	8.7–11.8	10.1	0.81
Caudal peduncle width	20	5.8	4.4–6.3	5.2	0.52
Caudal peduncle depth	20	14.4	13.4–15.0	14.2	0.47
Pectoral-fin length	20	19.4	18.6–23.1	20.2	1.07
Pelvic-fin length	20	20.4	14.8–21.8	19.5	1.38
Pre-dorsal length	20	44.3	43.9–49.8	45.9	1.45
Pre-anal length	20	64.7	59.5–64.7	62.5	1.07
Pre-pelvic length	20	43.5	38.3–43.7	41.6	1.52
Percentage of HL					
Snout length	20	48.0	40.4–55.2	46.7	4.24
Orbit diameter	20	24.0	19.8–31.3	25.6	3.17
Upper jaw length	20	30.1	25.4–35.6	30.0	2.33
Lower jaw length	20	35.3	35.0–38.9	36.6	1.22
Interorbital width	20	28.0	25.8–31.8	28.4	1.44
Preorbital depth	20	29.5	25.8–33.8	29.5	2.39
Caudal peduncle length/width	20	1.9	1.4–2.3	2.0	0.18
Caudal peduncle length/depth	20	0.8	0.6–0.8	0.7	0.06
Scales in lateral line	20	35 (1), 36 (4), 37 (10), 38 (4) (H), 39 (1)			
Scales: lateral line to dorsal fin	20	6 (17) (H), 7 (3)			
Gill rakers (lower limb 1st arch)	17	13 (8), 14 (9) (H)			
Vertebrae (precaudal + caudal)	28	13 + 16 = 29 (1), 13 + 17 = 30 (2), 14 + 16 = 30 (7), 14 + 17 = 31 (18) (H)			
Dorsal fin	27	XIV 14 (2), XV 13 (4), XV 14 (2), XVI 12 (1), XVI 13 (13) (H), XVI 14 (4), XVI 15 (1)			
Anal fin	27	VII 11 (16) (H), VII 12 (9), VII 13 (1), VIII 10 (1)			

bars on the flanks over bright orange to reddish-orange ground coloration. It is further distinguished from both *P. lamenabe* and *P. tsimoly*, in life and preservative, by the absence of bluish-gray to bluish-black lips, lower jaw, lower cheek, gular region, and belly. *Paretroplus nourissati* is further distinguished from *P. lamenabe* by a shallower body (38.1%–43.5% vs. 47.0%–54.3% in *P. lamenabe*), pelvic fins that do not extend to origin of the anal fin when adducted, and by a smaller adult size (up to 160 mm SL vs. regularly exceeding 180 mm SL in *P. lamenabe*). *Paretroplus nourissati* is further distinguished from *P. tsimoly* by the absence of enlarged, lobed lips. Only *P. lamenabe* and *P. nourissati* exhibit a lateral pigmentation pattern in which the central two bars, which converge below the lateral midline, are by far the most prominent. By contrast, in life and preservation, *P. tsimoly* exhibits a pigmentation pattern in which the posteriormost five (or four, as the bar on the caudal peduncle is sometimes pale) bars on the flanks are about equally prominent.

DESCRIPTION: Morphometric and meristic data presented in table 8. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 24C and 45–47. A shallow-bodied and elongate *Paretroplus* belonging to Clade F, which also includes *P. lamenabe* and *P.*

tsimoly (fig. 1). *Paretroplus nourissati* is recovered as the sister taxon to *P. tsimoly*, and this clade is in turn the sister taxon to *P. lamenabe*. *Paretroplus nourissati* is comparable in adult size to *P. tsimoly*, rarely exceeding 150 mm SL. Head pointed, snout and predorsal profile moderately curved, lending species a beaked appearance in lateral view. Premaxillary pedicels prominent, distinct notch present posterior to distal margins of ascending processes. Dorsal body outline mildly curved, ventral outline mostly straight, except posteriorly. Caudal peduncle short, deep, and laterally compressed. No sexually dimorphic features apparent; however, in photographs of breeding pair in de Rham and Nourissat (2004: 122), male appears to exhibit brighter and more vivid yellowish to orange coloration.

Total vertebral count 29 to 31 (mode 31), with formulae of: 13 + 16, 13 + 17, 14 + 16, and 14 + 17, precaudal and caudal vertebrae, respectively.

Jaws isognathous. Lips fleshy and well developed, but not lobed (i.e., fleshy medial flaps lacking on both upper and lower lips). Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, remaining upper-jaw teeth smaller and graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw usually number six to nine on each side, and total 13–16. Teeth in lower jaw number six or seven on each side, and total 12–14. Upper-jaw teeth comparatively closely set for *Paretroplus*. Lower-jaw teeth more or less widely set and evenly spaced.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; molariform teeth present posteromedially, but these teeth not particularly robust. LPJ weakly sutured (i.e., gap present posteriorly between right and left fifth ceratobranchial elements in specimens up to about 100 mm SL), with few weak interdigitations on posteroventral margin. Seven robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones (fig. 12C). Tooth plates not confluent with outer-row gill rakers of fourth ceratobranchial elements. Bases of some tooth plates becoming confluent with each other, but majority separate. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates robust and becoming nearly molariform posteromedially, hooked and bicuspid laterally and anteromedially. Anteromedial teeth becoming enlarged, but not molariform. Posteromedial teeth retain a weak apical cusp, even in larger specimens examined. Dentition on second pharyngobranchial tooth plates hooked and bicuspid and arrayed in two complete rows (occasionally, incomplete third row present).

Thirteen or 14 elongate triangular gill rakers arrayed along lower limb of first gill arch. Rakers on lower limb of first gill arch edentate to weakly denticulate medially. All other lower-limb rakers (i.e., those on gill arches 2–4) triangular and moderately to strongly denticulate dorsally. These rakers elongate compared to short, spherical rakers in members of Clade G, comprising deep-bodied *Paretroplus* (Clade I) and *P. kieneri* species complex (Clade H). Teeth on rakers of gill arches 2–4 thin, conical and curved distally near crown, but much shorter than body of raker. Epibranchial rakers on first gill arch elongate and thin, numbering 12.

Body covered with large, regularly imbricate, cycloid scales. Posterior field of lateral body scales thin and not ossified. Posterior field of head scales ossified. Well-developed scale ridges (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from spiny dorsal and anal fins, but becoming fused to membranes of both soft dorsal and anal (fig. 22B). On membranes between fin rays, multiple discrete rows of scales extend well beyond scale ridges and onto both soft dorsal and anal fins. Pelvic axillary scale present and well developed. Interpelvic

scale elongate and somewhat pointed terminally. Lateral-line scales number 35–39 (mode 37). Chest scales noticeably reduced in size and embedded (fig. 24C). Belly scales markedly reduced in size compared to chest scales, those along ventral midline smallest and very embedded (such that the belly appears asquamate). Multiple rows of scales, markedly reduced in size, extend on flanks from chest (and continue posteriorly dorsal to pelvic fins and anus) to about anal-fin origin (fig. 24C). Three to five (usually three or four) rows of scales on cheek. Opercle and subopercle scaled. Interopercle scaled only posteriorly or asquamate. Preopercle asquamate. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly about 3/4 length of fin on dorsal and ventral lobes, and about 1/3 length of fin medially.

Dorsal with XIV–XVI spines, 12–15 soft rays. Anal with VII–VIII spines, 10–13 soft rays. Origin of dorsal fin at about level of vertical through anterior margin of pectoral-fin insertion. Caudal fin weakly emarginate, margins of upper and lower lobes broad and rounded, and not produced. Pectoral fin broad and rounded at distal margin, rays slightly excised from fin terminally. Distal margins of soft dorsal and anal fins rounded, slightly produced in larger specimens, but with no trailing margins. Posterior margins of soft dorsal and anal fins terminate just anterior of caudal-fin origin in juveniles and extend slightly past origin in large adults (from about 120 mm SL). Pelvic fins terminate anterior to origin of anal fin when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital foramina present. Paired anterior gas bladder bullae with tough and thickened tunica externa, and anteriormost chambers firmly lodged in exoccipital recesses (fig. 20C). Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) lacking along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins (structures appear less well developed in *P. nourissati* and *P. tsimoly* than in other species of *Paretroplus*). Nasal bones elongate. Lower pharyngeal jaw (LPJ) with reduced number of interdigitations on ventral suture and indentation on ventral face of posterior horns. Interdigitations along ventral suture of LPJ shallow and weak. Posterior horns of LPJ narrow, particularly along ventrally projecting ridges, and gap present between left and right fifth ceratobranchial elements, posterior to ventral suture.

Coloration in Life: Pinkish-brown, grey, or reddish-brown (nonbreeding, sexually quiescent individuals) to bright yellowish-orange, orangish-red, or bright red (breeding, sexually active individuals) ground coloration, with two prominent vertical and generally converging (below the lateral midline) dark gray to jet black midlateral bars (de Rham and Nourissat, 2004: 122). Total of six or seven vertical bars present on flanks. Apart from two prominent midlateral bars, representing the second and third or third and fourth bars in series, remaining bars generally faint, although those on posterior region of flank easily visible. Fins gray, pinkish brown, or reddish brown and similar to base body coloration in nonbreeding individuals, and solid yellowish orange, orangish red, or bright red in breeding individuals. Lips, lower cheek, gular region, and belly very pale blue or grey in sexually active individuals (see photographs in de Rham and Nourissat, 2004: 122).

Coloration in Preservative: Body ground coloration reddish brown, golden brown, or dark grayish brown. Six or seven dark brown or blackish vertical bars present on flanks. Two midlaterally located bars most prominent and usually converging below lateral midline (figs. 24C, and 45–46). Apart from two prominent midlateral bars, remaining bars comparatively faint, although those on posterior flank readily visible. Body somewhat darker overall dorsally. Dark gray, golden brown, or brownish triangular patch easily visible in pectoral-fin axil in most specimens (faint in others). Unpaired fins

olive, brown, or grayish. Pectoral fins olive or gray. Pelvic fins tan, brown, or light grey. Lower lip, lower cheek, and gular region ranges from pale yellow, to olive, to light brown. Upper lip ranges from pale yellow to dark grayish brown. Juvenile specimens strongly barred (to about 70 mm SL), with series of lateral bars prominent over entire flank (vs. only two midlateral bars strongly pigmented in adults) (fig. 47).

DISTRIBUTION AND HABITATS: The known range of *P. nourissati* is restricted, encompassing only the Amboaboa and Mangarahara rivers near their confluence, which is in the vicinity of the town of Mandritsara in northeastern Madagascar (fig. 48). The species is also reported to occur in neighboring lakes, located a few kilometers from the confluence of the Mangarahara and Amboaboa rivers (de Rham and Nourissat, 2004: 121–122). The Amboaboa River is a tributary of the Mangarahara River, which itself is a moderately sized left-bank tributary of the extensive westward flowing Sofia drainage. *Paretroplus nourissati* co-occurs in these rivers with *P. gymnopreopercularis*; neither species has been collected to date from the Sofia River proper. Ichthyological surveys in this remote region of Madagascar have not been extensive and *P. nourissati* could potentially be more widespread in distribution.

The Amboaboa and Mangarahara rivers near the type locality are shallow, clear (low in turbidity), and the current is swift, with many areas of small cascades and riffles. These rivers flow over large areas of exposed bedrock, and the substrate is generally rocky, with many exposed boulders, and interspersed with areas of sand. *Paretroplus nourissati* frequents shallow, rocky stretches with a swift current and riffles. The species is frequently collected in swift-flowing water only a few inches deep, where it hides under rocks.

Although not widespread in distribution, in the mid-1990s *P. nourissati* was still relatively common within its limited range in the Mangarahara and Amboaboa rivers. Nevertheless, in consideration of its very restricted distribution, *P. nourissati* would seem to be vulnerable to increased fishing pressure and continued habitat degradation. Unfortunately, de Rham and Nourissat (2004) report that on their most recent visit to the region (in 1999) they found the Mangarahara River upstream from its confluence with the Amboaboa River to be completely dry due to the combined effects of a prolonged drought in the region and water diversion to irrigate rice fields year-round via an upstream dam (for additional information see Distribution and Habitats for *P. gymnopreopercularis* below). Subsequent ichthyological surveys of the Amboaboa River found *P. nourissati* to be abundant in 2004, but greatly reduced in numbers in 2006, possibly as a consequence of the many years of severe drought that the region has experienced (P. Loiselle, personal commun.).

LOCAL NAME: *Lamena*, a Malagasy word, which translates literally as "the red one".

ETYMOLOGY: The species was named in honor of the French aquarist, naturalist, and intrepid traveler Jean-Claude Nourissat, who with Patrick de Rham discovered the species (in 1991) and collected the type specimens.

RELATIONSHIPS AND DISCUSSION: Based on the simultaneous analysis of morphological features and nucleotide characters, *P. nourissati* is recovered as a member of Clade F and as the sister taxon to *P. tsimoly* (fig. 1). Clade F is diagnosed by two unambiguously optimized morphological transformations, the first of which is unique and unreversed, the presence of two prominent and converging midlateral bars (several fainter bars are also present on the flanks) (figs. 24C, and 45–46) and elongate nasal bones. *Paretroplus damii* is recovered as the sister taxon to Clade F. Clade E, comprising *P. damii*, *P. tsimoly*, *P. nourissati*, and *P. lamenabe*, is united by five unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1).

Paretroplus nourissati was originally described as the type species of a new genus, *Lamena* Allgayer, 1998, and represented the first member of the "lamena" group (Clade F) to be discovered. The results of a number of systematic studies that followed soon thereafter indicated that *Lamena nourissati* was nested within *Paretroplus*, and it was argued that *Lamena* be synonymized with

Paretroplus Bleeker, 1868 (Sparks and Reinthal, 1999; Sparks, 2001; Stiassny et al., 2001; Sparks, 2004a; Sparks and Smith, 2004). *Paretroplus damii* Bleeker, 1868 is the type species of the genus, and is the sister taxon to Clade F, which includes *P. nourissati*. Synonymy of *Lamena* with *Paretroplus* reinstated *Paretroplus* as a monophyletic assemblage.

Although members of Clade F are very similar morphologically, sexually active (breeding) individuals of *Paretroplus nourissati* exhibit a diagnostic pigmentation pattern consisting of broad vertical black bars on the flanks over bright orange to reddish-orange ground coloration. *Paretroplus nourissati* is further distinguished from the other members of Clade F, *P. lamenabe* and *P. tsimoly*, in life and preservative, by the absence of dark bluish-gray to bluish-black lips, lower jaw, lower cheek, gular region, and belly. Although this region may be pale blue or very pale gray in breeding *P. nourissati* (see photographs of aquarium specimens in de Rham and Nourissat, 2004: 122), it is never darkly pigmented. Additionally, *P. nourissati* can be distinguished from *P. lamenabe* by a shallower body (38.1%–43.5% vs. 47.0%–54.3% in *P. lamenabe*), shorter pelvic fins that do not extend to anal-fin origin when adducted, and by a smaller adult size (<160 mm SL vs. regularly >180 mm SL in *P. lamenabe*). *Paretroplus nourissati* is further distinguished from *P. tsimoly* by the absence of markedly enlarged and lobed lips. *Paretroplus nourissati* and *P. lamenabe* are unique in sharing a lateral pigmentation pattern, in life and preservation, in which the central two bars, which converge below the lateral midline, are the most strongly pigmented (vs. the posteriormost five [or four, as the bar on the caudal peduncle is sometimes pale] bars on the posterior flanks about equally prominent in *P. tsimoly*). *Paretroplus nourissati* and *P. tsimoly* can generally be distinguished from *P. lamenabe* by tooth count in the upper jaw (13–16 and 12–14 in *P. nourissati* and *P. tsimoly*, respectively, vs. 15–18 in *P. lamenabe*), and by a much lesser degree of squamation extending onto the soft dorsal and anal fins. Stiassny et al. (2001) report a range of 14–20 teeth in the upper jaw for *P. nourissati*; however, I have not been able to find a specimen with more than a total of 16 upper-jaw teeth.

All members of Clade F share two features of the lower pharyngeal jaw (LPJ) that were noted by Stiassny et al. (2001: 37–38, fig. 9), a reduced number of interdigitations on the ventral suture (posteroventral margin of LPJ) and an indentation on the ventral face of the posterior horns. In addition, the interdigitations along the ventral suture of the LPJ in members of Clade F are shallow and weak. Members of Clade F are also united by the presence of posterior horns on the LPJ that are very narrow, particularly along the ventrally projecting ridges, and by the presence of a narrow gap between left and right fifth ceratobranchial elements, posterior to the ventral suture.

Members of Clade E, which includes Clade F and *P. damii*, are unique among *Paretroplus* in sharing a number of apomorphic features related to scale morphology and squamation pattern. Uniquely in members of Clade E, the posterior field of the lateral body scales is unossified and feeble (fig. 22B), multiple discrete rows of scales extend onto the membranes of both the soft dorsal and anal fins (fig. 24C), the chest scales are distinctly reduced in size and quite embedded, and multiple rows of scales of reduced size extend posteriorly from the chest (dorsal to the pelvic fins and anus) to about anal-fin origin (figs. 45–46). Within *Paretroplus*, members of Clade F exhibit a squamation pattern on the chest and belly in which the scales are both more reduced in size and more highly embedded than in other members of the genus, including *P. damii*, lending the ventral chest and belly an asquamate appearance.

Paretroplus maromandia Sparks and Reinthal, 1999

Figures 35, 49–50; plate 1H; table 9

Paretroplus aff. *maromandia* from Lake Andrapongy and the Anjingo-Ankofia River: de Rham and Nourissat, 2004: 109–110.

Paretroplus aff. *maromandia* from the Maevarano River: de Rham and Nourissat, 2004: 107–108.

HOLOTYPE: UMMZ 234790, holotype, adult, likely male (sex indeterminate due to poor internal preservation), 126.9 mm SL;

Fig. 49. *Paretroplus maromandia*, holotype, UMMZ 234790, 126.9 mm SL; northwestern Madagascar: Mahajanga Province: region of Ambanja: immediately south of village of Maromandia: Maintsomalaza River.

Fig. 50. *Paretroplus maromandia*, nontype specimen, MHNG 2623.080, 119.9 mm SL; northwestern Madagascar: Mahajanga Province: region of Ambanja: near town of Maromandia: Manongarivo River.

TABLE 9
Morphometric and meristic data for *Paretroplus maromandia*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

		P. maromandia			
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	6	126.9	113.0–129.7	121.9	
Percentage of SL					
Head width (max.)	6	15.8	15.2–16.3	16.0	0.38
Head length	6	29.3	28.9–31.0	29.8	0.80
Body depth	6	60.1	57.6–60.1	58.9	1.03
Caudal peduncle length	6	6.2	6.2–7.4	6.6	0.42
Caudal peduncle width	6	4.3	3.7–4.3	4.1	0.25
Caudal peduncle depth	6	16.7	15.8–16.9	16.5	0.39
Pectoral-fin length	6	20.4	20.4–25.0	22.3	1.43
Pelvic-fin length	6	22.4	22.2–24.0	22.7	0.60
Last dorsal spine length	2	17.0	15.5–17.0	16.3	0.77
Pre-dorsal length	4	N.A.	44.3–48.5	46.2	1.53
Pre-anal length	4	N.A.	57.7–59.5	58.8	0.73
Pre-pelvic length	4	N.A.	39.6–41.3	40.1	0.70
Percentage of HL					
Snout length	6	46.2	44.2–46.5	45.2	0.90
Orbit diameter	6	31.5	29.1–32.2	30.6	1.01
Upper jaw length	6	28.0	26.8–28.6	27.7	0.69
Lower jaw length	6	33.6	32.8–35.6	33.8	0.94
Interorbital width	6	33.3	32.3–34.6	33.4	0.74
Preorbital depth	6	32.8	31.3–32.8	32.4	0.59
Caudal peduncle length/width	6	1.4	1.4–1.9	1.6	0.18
Caudal peduncle length/depth	6	0.4	0.4–0.5	0.4	0.03
Scales in lateral line	6	39 (2), 40 (3), 41 (1) (H)			
Scales: lateral line to dorsal fin	6	7 (1) (H), 8 (5)			
Gill rakers (lower limb 1st arch)	6	10 (6)			
Vertebrae (precaudal + caudal)	6	14 + 18 = 32 (1), 15 + 18 = 33 (3), 16 + 18 = 34 (2) (H)			
Dorsal fin	6	XV 21 (1), XVI 20 (2), XVI 21 (2), XVI 23 (1) (H)			
Anal fin	6	VIII 14 (1), IX 14 (2), IX 15 (2) (H), IX 16 (1)			

northwestern Madagascar: Province of Mahajanga: region of Ambanja: immediately south of village of Maromandia: Maintsomalaza River, near confluence of Adranomalaza and Manongarivo rivers, downstream from where rivers unite: 14°12′S, 48°04′E; JSS 96-13; obtained from fisherpersons; J. S. Sparks, K. J. Riseng, and Richard Randriamampionina, 7-VII-1996.

PARATYPE: AMNH 227336, 1 ex., juvenile, presumably female (gonads reasonably well developed with abundant lipids, although no oocytes detected), 113.0 mm SL; data as for holotype.

ADDITIONAL NONTYPE MATERIAL EXAMINED: MHNG 2537.60, 2 ex. (1 dried), 93.7–130.0 (approx./dried) mm SL; northwestern Madagascar: region of Antsohihy: Ankofia River drainage: Lake Andrapongy; P. de Rham and J.-C. Nourissat, 17-X-1992. MHNG 2623.080, 3 ex., 1 ex. C&S, 119.8–121.8 mm SL; northwestern Madagascar: Region of Ambanja: near town of Maromandia: Manongarivo River, region of mouth of Manandtritzara [sic] River; P. de Rham and J.-C. Nourissat, 22-X-1999. MHNG 2640.041, 1 ex., 129.7 mm SL; northwestern Madagascar: region of Ambanja: near town of Maromandia: Andranomalaza River; P. de Rham and J.-C. Nourissat, X-1999.

DIAGNOSIS: *Paretroplus maromandia* is a member of the deep-bodied clade of *Paretroplus* (Clade I) and the only member of the

genus, apart from *P. polyactis*, in which the entire lateral series of bars is prominent, including in adults. It is the only species of *Paretroplus* occurring in western drainages with strong lateral barring. *Paretroplus maromandia* is distinguished from *P. polyactis* by the presence of lateral bars that extend more or less over the entire flank, from the dorsal-fin base (and sometimes extending onto the fin membrane itself) to the anal-fin base (vs. bars that terminate approximately under the lateral midline and do not extend to the anal-fin base in *P. polyactis*), by a greater lateral-line scale count (39–41 vs. 31–36 in *P. polyactis*), fewer gill rakers on the lower limb of the first arch (10 vs. 11–13 in *P. polyactis*), a higher dorsal-fin ray count (20–23 vs. 15–18 in *P. polyactis*), and by bright yellow to greenish-yellow body ground coloration interrupted by seven prominent, solid black vertical bars on the flanks (vs. bars and intervening regions highly speckled/spotted and resembling a chain-link fence, owing to pigmentation pattern in which scale margins are markedly darker than centers in *P. polyactis*). In life, *P. maromandia* is further distinguished from *P. polyactis* by a golden iris (vs. red), and the presence of vivid red pigmentation on the flanks, below the lateral midline.

DESCRIPTION: Morphometric and meristic data presented in table 9. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 49–50. A deep-bodied, laterally compressed *Paretroplus* belonging to Clade I, which comprises all deep-bodied and essentially disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. menarambo*, *P. petiti*, and *P. polyactis*) (fig. 1). Body laterally compressed and deep. Head blunt and steeply sloping in lateral view. Predorsal head profile moderately to strongly curved. Interorbital protuberance producing distinct concavity rostral to orbit. Lateral snout outline more or less straight, forming angle of approximately 50° to horizontal. Caudal peduncle short, deep, and laterally compressed. No sexually dimorphic features readily apparent.

Total vertebral count 32–34 (mode 33), with formulae of: 14 + 18, 15 + 18, and 16 + 18 precaudal and caudal vertebrae, respectively.

Jaws isognathous and short, both upper and lower jaws bearing tiny, fleshy papillae. Single row of spatulate unicuspid teeth, generally widely and irregularly set, in both upper and lower jaws. Teeth wide and flattened at crown, and procumbently implanted. In upper jaw, dentition restricted to anterior portion of premaxillary arcade. Tooth on each side of premaxillary symphysis markedly enlarged; these symphyseal teeth closely set. Other upper-jaw teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but somewhat reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Including symphyseal teeth, teeth in upper jaw number five to seven on either side. Upper-jaw teeth laterally graded in size and widely set. Lower-jaw teeth, including those at symphysis, number seven to 10 in total. Lower-jaw teeth not uniform in size or spacing. Posteriormost two lower-jaw teeth reduced in size (i.e., anteromedial teeth not graded in size laterally). Dentition restricted to anterior portion of dentary.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. Hooked and bicuspid peripheral LPJ teeth numerous and closely set, whereas enlarged medial and molariform posteromedial teeth widely and/or irregularly set. LPJ well sutured, with numerous interdigitating sutures on posteroventral margin. Eight robust tooth plates cover majority of dorsal surface of fourth ceratobranchial elements; anteromedial tooth plates abut each other, whereas those on posterior half of fourth ceratobranchial not confluent. Tooth plates not confluent with outer-row (= lateral) gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid both laterally and anterome-

dially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, closely set, and arrayed in four rows.

Ten robust, triangular, and rather stout gill rakers closely arrayed along lower limb of first gill arch, excluding raker located in angle of arch; anteriormost one or two rakers somewhat reduced in size. These ceratobranchial gill rakers denticulate dorsomedially. All other lower-limb rakers (i.e., those on gill arches 2–4) short, stout, and strongly denticulate dorsally. Epibranchial gill rakers of first arch elongate and slender, and number 10–12.

Body covered with large, regularly imbricate, cycloid scales from level of orbit to base of caudal fin. Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from both spiny and soft portions of dorsal and anal fins (figs. 49–50). Pelvic axillary scale present and well developed. Interpelvic scale elongate and tapered distally. Lateral line scales number 39–41 (mode 40). Chest scales only slightly reduced in size compared to flank scales, and weakly embedded. Belly scales along ventral midline markedly reduced in size and embedded; much smaller than flank and chest scales. Cheek scales arrayed in oblique series, extending from ventral margin of midorbit to ventral margin of preopercle, and numbering six to seven rows. Snout, lacrimal, and anterior portion of interorbital region asquamate. Preopercle scaled anteriorly, asquamate ventrally and along posterior margin of shaft. Opercle and subopercle fully scaled; interopercle fully scaled except at rostral margin. Scales on caudal fin reduced in size and extending to about 3/4 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XV–XVI spines, 20–23 soft rays. Anal with VIII–IX spines, 14–16 soft rays. Origin of dorsal fin located somewhat posterior to vertical through pectoral-fin insertion (in closely related congeners, dorsal-fin origin at about level of pectoral-fin insertion). Origin of dorsal fin located slightly anterior to pelvic-fin insertion. Caudal margins of both the soft dorsal and anal fins notably rounded, extend only slightly beyond origin of caudal fin. Caudal fin emarginate and crescent shaped, trailing margins of upper and lower lobes slightly produced, lending forked appearance to fin. Pelvic fins extend just past origin of anal fin when adducted.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital foramina present. Paired anterior gas bladder bullae with tough, thickened tunica externa and narrow tubular connections (= diverticula) to main gas bladder chamber. Anteriormost chambers firmly lodged in exoccipital recesses. Expansive, wide and rounded excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

Coloration in Life: Base body coloration bright yellow, greenish yellow, or olive. Seven prominent and broad black vertical bars present on flanks (anteriormost bar sometimes considerably weaker than rest, but always visible). Bars extend anteroposteriorly from caudal margin of opercle to caudal peduncle, and generally extend over entire flank, from dorsal-fin base (and sometimes extending onto fin membrane itself) to anal-fin base. Head and opercular region golden, golden brown, or greenish brown. Vivid red spotting on flanks, generally restricted ventral to lateral midline and concentrated anteriorly, posterior to pectoral-fin base. Red pigmentation may extend onto opercle and subopercle. Red flank pigmentation generally interrupted by dark lateral bars, but sometimes partially occluding anterior bars (see color photographs in de Rham and Nourissat, 2004: 103–109). In juveniles, red spotting covers entire flank (see photograph in de Rham and Nourissat, 2004: 104). Interorbital region gray. Snout golden, golden brown, greenish brown, or gray. Gular region, chest, belly and ventrum ranges from bright yellow, to gray, to nearly black. Grayish or black pigment may extend posteriorly along ventrum and dorsal to anal-fin base. Lips gray to dark gray. Dorsal and anal

fins generally dark charcoal gray, both with thin red terminal band. Caudal fin dark gray proximally, becoming lighter at distal margin of fin, and fringed in red terminal band. Pelvic fins dark gray to blackish. Pectoral fins gray to dark charcoal. Solid black patch present in pectoral-fin axil, visible as black crescent when fin adducted. All fins, except pectorals, with slight reddish tinge in life.

Coloration in Preservative: Base body coloration tan, with some golden-brown hues, to golden brown. Red pigmentation on flanks lost in alcohol. Overall body pigmentation is somewhat darker dorsally, becoming lighter ventrally. Seven distinct, dark brown to black vertical bands present on flanks, extending from posterior margin of head to caudal peduncle (figs. 49–50). Bands most pronounced medially and dorsally on flanks, but extend over entire flank. Head and opercular region golden brown, dark brown, or grayish. Interorbital region, lacrimal, and snout dark brown to dark grayish brown. Lower lip, gular region, and lower portion of opercular series yellowish to golden brown. Upper lip yellowish to grayish brown. Chest and belly golden brown to dark grayish brown. Dorsal fin light grayish brown to dark brown. Anal fin a darker grayish brown to charcoal. Caudal fin tan, golden brown, or medium brown, and similar to flank ground coloration. Pelvic fins similar in coloration to the anal fin, dark grayish brown to charcoal overall, although leading edge and posterior rays tan or golden brown. Pectoral fins mostly hyaline, rays light tan to golden brown. Black patch present in pectoral-fin axil.

Viscera and Diet: Radiographs of holotype and paratype reveal that *P. maromandia* feeds primarily on small gastropods, as gut of each specimen was tightly packed with crushed shells. Presence of robust molariform pharyngeal dentition also consistent with this feeding behavior.

Distribution and Habitats: The type series of *P. maromandia* was collected from the Maintsomalaza River, which is the local Malagasy name for the river just downstream from the confluence of the Manongarivo and Andranomalaza rivers, in the immediate vicinity of the town of Maromandia (14°12′S, 48°04′E) along the northwest coast of Madagascar (fig. 35). At the time of collection of the type series, corresponding to the dry season, this large, tidally influenced river was generally shallow, and the water was relatively clear, with a moderate current. The substrate comprised mostly sand and silt, although in places was extremely muddy. In addition to the Maintsomalaza River, local fishermen report catches of the new species from estuaries in the area and from the Andranomalaza River (Nourissat, 1998).

Specimens that appear to be referable to *P. maromandia* have also been collected to the south of the Andranomalaza-Manongarivo drainage basin, from both the Maevarano River and Lake Andrapongy, a shallow floodplain lake located within the Ankofia River drainage basin. Although Sparks and Reinthal (1999) did not have material to examine from either locality at the time of their description, Sparks (personal obs.) did observe a dried/smoked specimen from Lake Andrapongy during a visit in 1994, which seemed to resemble *P. maromandia* in terms of body shape and the presence of a prominent vertical barring pattern. Subsequently, I have been able to examine two specimens (one dried/smoked) from that locality (MHNG 2537.60, 93.7–130.0 mm SL) collected by de Rham and Nourissat in 1991. Although the single specimen that is not dried is only a juvenile (93.7 mm SL), and much smaller than any available specimen of *P. maromandia* from the Andranomalaza-Manongarivo drainage basin, I an unable to find any morphological features to distinguish this individual from topotypic *P. maromandia* (apart from body depth, which is likely an artifact of its smaller size). Regrettably, de Rham and Nourissat (2004: 109) report that this population is now presumed extinct. No preserved material from the Maevarano River seems to have been deposited in museum collections (de Rham, personal commun.), although the color photographs presented in de Rham and Nourissat (2004: 107–108) closely resemble *P. maromandia* in the possession of a prominent vertical barring pattern and vivid red pigmentation on the flanks. In the absence of evidence to the contrary, the Maevarano River population is herein con-

sidered to be conspecific with *P. maromandia*. In summary, the range of *P. maromandia* includes, from north to south, the Andranomalaza-Manongarivo drainage basin, the Maevarano River, and formerly, Lake Andrapongy, within the Ankofia drainage basin. The species has never been collected from the Ankofia or Anjingo rivers proper, and Lake Andrapongy presumably represented its southern range limit. Based on collection locality data, *P. maromandia* appears limited to the lower reaches of large tidally influenced rivers, estuaries, and shallow floodplain lakes (i.e., Lake Andrapongy) that experience periodic connections to the sea during the wet season (Sparks and Reinthal, 1999; de Rham and Nourissat, 2004). Apart from the former Lake Andrapongy population, the species has not been collected upstream of tidally influenced sections of rivers within its range.

Paretroplus maromandia exhibits a very distinct pigmentation pattern and coloration. The additional populations from the Maevarano River and Lake Andrapongy, which were not part of the type series, share these distinctive features. Tissue vouchers were not available from either of these populations, and they could not be included in molecular phylogenetic analyses. Regardless, specimens from these two populations cannot currently be distinguished from topotypic *P. maromandia* on the basis of apomorphic morphological features and, therefore, there is no evidential basis for considering them not to be conspecific with *P. maromandia*.

Given that *P. maromandia* has only recently been discovered and that the surrounding region is poorly surveyed for freshwater fishes, little is known regarding the current status of this species. If *P. maromandia* can tolerate estuarine conditions, as indicated by collection-locality data, including the type locality, this species may not be as critically endangered as other members of *Paretroplus*, which exhibit highly restricted inland distributions, frequently comprising but a single basin. It has been hypothesized that estuaries serve as refugia for native Malagasy species (Reinthal and Stiassny, 1991). Apart from *P. maromandia*, the only additional species of *Paretroplus* occurring almost exclusively in the tidally influenced portions of coastal rivers, or in estuarine conditions, is the widespread and still relatively common *P. polyactis*, which ranges along nearly the entire eastern coast of Madagascar (fig. 33). Regardless, throughout its limited range, *P. maromandia* seems nowhere abundant or even common and few collections have been made (there are only a handful of specimens in museum collections available for study, all of which have been examined here).

The region surrounding Maromandia, both to the north and south, is in need of comprehensive ichthyological surveys. The Tsaratanana Massif, the highest point in Madagascar (Maromakotro, 2876 m), is located inland to the north of Maromandia, and still contains large sections of intact rainforest that are difficult to access. The massif also creates what has been referred to as the Sambirano (micro-) climate (extending westward to the satellite island of Nosy Be), which is notably wetter than the dry western climate immediately to the south.

LOCAL NAME: *Damba* or *damba mena*. *Damba* is the Malagasy name used generally to refer to the deep-bodied species of *Paretroplus* throughout the northwest of Madagascar, and *mena* is Malagasy for "red", in reference to the vivid red flank pigmentation characteristic of this species.

ETYMOLOGY: Named for the town and general region from which the species was first collected. In English, the Malagasy prefix *maro-* translates as "many", and the Malagasy suffix *-mandia* means "to tread on or to go on a way/journey". The epithet, *maromandia*, is used as a noun in apposition.

RELATIONSHIPS AND DISCUSSION: *Paretroplus maromandia* is a member of Clade I, comprising all the deep-bodied and more or less disk-shaped members of *Paretroplus* (also including *P. dambabe*, *P. maculatus*, *P. menarambo*, *P. petiti*, and *P. polyactis*), which is supported by three unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1). Apart from pigmentation pattern and coloration, all members of this clade are morphologically very similar.

In the combined analysis of morphological features and nucleotide characters, *P. maromandia* is recovered in an unresolved polyt-

omy with all other deep-bodied species of *Paretroplus* that have distributions restricted to western basins (fig. 1: Clade J). Monophyly of Clade J, comprising *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*, is supported by two unambiguously optimized morphological features, the second of which is unique and unreversed: the presence of a blunt snout with a steeply sloping profile in lateral view and a distinctive lateral pigmentation pattern comprising alternating horizontal light and dark stripes (fig. 50). A lack of resolution within Clade J is due to the fact the *P. petiti* (known only from the formalin-fixed holotype) is included on the basis of morphological features only, which are insufficient for resolving relationships within this anatomically conservative clade. In a combined analysis of morphological features and nucleotide characters that specifically excluded *P. petiti*, *P. maromandia* is recovered as the sister taxon to *P. menarambo* (fig. 2), a result also obtained by the analysis of nucleotide characters only (Sparks, 2004a; Sparks and Smith, 2004).

In addition to considerable differences in pigmentation pattern and coloration, *P. maromandia* is distinguished from *P. menarambo* by number of scales in the lateral line (39–41 vs. 34–38 in *P. menarambo*), and usually by the number of gill rakers on the lower limb of the first arch (10 vs. 9 in *P. menarambo*; 2 of 20 specimens had a count of 10 in *P. menarambo*). Moreover, in *P. menarambo* the caudal fin is considerably more lunate, with elongate trailing dorsal and ventral filaments in large specimens, and a concave, rounded caudal margin. In *P. maromandia*, the caudal margins of both the soft dorsal and anal fins are deep bodied and notably rounded compared to congeners of similar standard length (i.e., >100 mm SL; figs. 49–50), a feature it shares only with *P. maculatus*. In similarly sized specimens of *P. maculatus*, however, the caudal margin of the anal fin is somewhat more pointed than in *P. maromandia*.

Paretroplus maromandia and *P. menarambo* are the only species of *Paretroplus* with a dorsal-fin ray count that exceeds 20 (range 20–23 in *P. maromandia* and 19–21 in *P. menarambo*). Otherwise, only *P. maculatus* has a dorsal-fin ray count that reaches 20 (range 16–20).

Paretroplus tsimoly Stiassny, Chakrabarty, and Loiselle, 2001
Figures 48, 51–52; plate 1I; table 10

HOLOTYPE: AMNH 229558, 140.3 mm SL, adult female; northwestern Madagascar: Majunga (= Mahajanga) Province: Betsiboka River drainage basin: Akalimilotrabe River (= Kalamilotra or Kamilotra River) at village of same name, ca. 43 km northwest of Maevatanana: 16°48′ 8.0″S, 47°00′57.0″E: alt. 318 m a.s.l.; P. V. Loiselle, 7-VI-1997.

PARATYPES: AMNH 229559, 2 ex., 1 ex. C&S, 99.3–138.1 mm SL, larger specimen adult female, smaller indeterminate sex; data as for holotype. MNHG 2609.44, 1 ex. 127.2 mm SL, adult female; data as for holotype; not examined. UMMZ 236893, 1 ex., 123.6 mm SL, adult female; data as for holotype.

ADDITIONAL NONTYPE MATERIAL EXAMINED: AMNH 229556, 2 ex., 110.1–129.5 mm SL, adult males; northwestern Madagascar: Mahajanga Province: region of Maevatanana: Betsiboka drainage (but with no more specific locality data). AMNH 229557, 1 ex. C&S, 52.0 mm SL, juvenile; data as for holotype. MHNG 2640.038, 2 ex., 133.6–137.0 mm SL; northwestern Madagascar: Mahajanga Province: Kamoro River at Antsalahina; P. de Rham and J.-C. Nourissat, 20-X-2001. AMNH 238563, 1 ex., 120.6 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: Kanero/Kamoro River; JSS 37-2003; J.-C. Nourissat, C. Toumy, and J. Andriamianamihaja, X-2003. AMNH 238564, 1 ex., tissue voucher specimen, 89.7 mm SL; northwestern Madagascar: Mahajanga Province: Betsiboka River drainage basin: Kamoro River; JSS 38-2003, EE-1-2003; J.-C. Nourissat, C. Toumy, and J. Andriamianamihaja, X-2003.

DIAGNOSIS: *Paretroplus tsimoly* is distinguished from all congeners in life and preservation by the possession of markedly enlarged, lobed bluish-gray to bluish-black (in life) or dark bluish-gray (in preservation) lips in adults. In addition, *P. tsimoly*, is distinguished from all congeners except *P. lamenabe* and *P. nourissati* by the presence of two wide, dark brown to black midlateral bands that converge below the lateral mid-

Fig. 51. *Paretroplus tsimoly*, holotype, AMNH 229558, 140.3 mm SL; northwestern Madagascar: Mahajanga Province: Akalimilotrabe River (= Kalamilotra River).

line, representing the second and third, or third and fourth, bars in series. *Paretroplus tsimoly* is further distinguished from both *P. lamenabe* and *P. nourissati* by a lateral pigmentation pattern in which the posteriormost five (or four, as the bar on the caudal peduncle is sometimes pale) bars on the flank are about equally prominent (vs. only central two bars strongly pigmented and prominent in *P. lamenabe* and *P. nourissati*).

DESCRIPTION: Morphometric and meristic data presented in table 10. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 51–52. A shallow-bodied and elongate *Paretroplus* belonging to Clade F, which also includes *P. lamenabe* and *P. nourissati* (fig. 1). *Paretroplus tsimoly* is recovered as the sister taxon to *P. nourissati*, and this clade is in turn the sister taxon to *P. lamenabe*.

Fig. 52. *Paretroplus tsimoly*, nontype specimen, AMNH 238563, 120.6 mm SL; northwestern Madagascar: Mahajanga Province: upper Kamoro River.

TABLE 10
Morphometric and meristic data for *Paretroplus tsimoly*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

		P. tsimoly			
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	8	140.3	89.7–140.3	124.9	
Percentage of SL					
Head width (max.)	7	18.3	17.2–18.8	18.1	0.52
Head length	7	34.8	32.3–35.4	34.6	0.95
Body depth	7	45.1	41.1–46.8	44.5	1.69
Caudal peduncle length	7	6.1	6.1–9.5	7.9	1.04
Caudal peduncle width	7	4.2	3.8–5.2	4.7	0.50
Caudal peduncle depth	7	15.4	14.1–15.7	15.1	0.55
Pectoral-fin length	7	21.9	20.2–22.9	21.6	0.83
Pelvic-fin length	7	20.9	20.5–23.2	21.4	0.86
Pre-dorsal length	7	47.6	43.9–48.3	46.3	1.42
Pre-anal length	7	63.2	61.4–63.3	62.6	0.64
Pre-pelvic length	7	40.4	40.4–43.3	41.7	0.85
Percentage of HL					
Snout length	7	51.2	32.1–54.6	48.0	7.03
Orbit diameter	7	23.8	22.1–28.5	24.8	2.04
Upper jaw length	7	32.2	28.5–32.6	30.9	1.28
Lower jaw length	7	36.1	32.9–37.7	35.3	1.33
Interorbital width	7	30.3	27.6–31.5	29.5	1.26
Preorbital depth	7	34.4	28.4–34.4	31.6	1.96
Caudal peduncle length/width	7	1.4	1.4–2.0	1.7	0.20
Caudal peduncle length/depth	7	0.4	0.4–0.6	0.5	0.06
Scales in lateral line	8	36 (1), 37 (2), 38 (4) (H), 39 (1)			
Scales: lateral line to dorsal fin	7	6 (2), 6.5 (1), 7 (4) (H)			
Gill rakers (lower limb 1st arch)	8	12 (1), 13 (5), 14 (2) (H)			
Vertebrae (precaudal + caudal)	6	14 + 17 = 31 (5) (H), 14 + 18 = 32 (1)			
Dorsal fin	6	XV 14 (1), XVI 13 (1), XVI 14 (2) (H), XVII 13 (2)			
Anal fin	7	VII 11 (2), VII 12 (2) (H), VIII 11 (3)			

Preserved material of *P. tsimoly* available for study is more or less comparable in size to *P. nourissati*, reaching a maximum size of less than 150 mm SL, but *P. tsimoly* possesses a noticeably deeper and more robust body. Although the holotype (140.3 mm SL) is the largest preserved specimen, de Rham and Nourissat (2004: 124) state that *P. tsimoly* can be distinguished from *P. nourissati* by a larger adult size. In addition, Stiassny et al. (2001: 35) report that field observations reveal that *P. tsimoly* regularly exceeds 200 mm SL. Head pointed, snout and predorsal profile moderately curved, giving species a beaked appearance in lateral view. Premaxillary pedicels prominent, and notch present posterior to distal ends of ascending processes in some specimens. Dorsal body outline mildly curved, ventral outline mostly straight, except posteriorly. Caudal peduncle short, deep, and laterally compressed. No sexually dimorphic characters apparent in preserved material available for study.

Total vertebral count 31 or 32 (mode 31), with formulae of: 14 + 17 and 14 + 18 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Lips quite fleshy and well developed. Fleshy medial flaps present on both upper and lower lips. Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, remaining teeth smaller and graded in size laterally. Lower-jaw teeth at symphysis not

enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw number 12–14 in total, and those in lower jaw number 12 or 13 in total (also see Stiassny et al., 2001). Upper-jaw teeth generally closely set, but also irregularly set. Lower-jaw teeth generally widely set, but also irregularly set in places.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; molariform teeth present posteromedially. LPJ weakly sutured, with few weak interdigitations on posteroventral margin. As in *P. lamenabe* and *P. nourissati*, apart from weak interdigitations, gap present posteriorly between right and left fifth ceratobranchial elements. Seven or eight robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Bases of some tooth plates becoming confluent with each other, but majority separate. Tooth plates not confluent with outer-row gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates becoming molariform posteromedially, although most posteromedial teeth not molariform and retain an apical cusp. Dentition on third upper pharyngobranchial tooth plates hooked and bicuspid laterally and anteromedially. Anteromedial teeth enlarged, but not molariform. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in two or three (two complete) rows.

Twelve to 14 triangular and somewhat elongate gill rakers arrayed along lower limb of first gill arch. Rakers on lower limb of first gill arch denticulate dorsomedially. All other lower-limb rakers (i.e., those on gill arches 2–4) triangular and moderately to strongly denticulate dorsally. These rakers elongate compared to short, spherical rakers in members of Clade G, comprising deep-bodied *Paretroplus* (Clade I) and *P. kieneri* complex (Clade H). Teeth on rakers of gill arches 2–4 thin, conical and curved distally near crown, but much shorter than body of raker. Epibranchial rakers on first gill arch markedly elongate and slender, numbering nine or 10 (also see Stiassny et al., 2001).

Body covered with large, regularly imbricate, cycloid scales. Posterior field of lateral body scales thin and not ossified (fig. 23C). Posterior field of head scales ossified. Well-developed scale ridges (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from spiny dorsal and anal fins, but becoming fused to membranes of both soft dorsal and anal. On membranes between fin rays, multiple discrete rows of scales extend well beyond scale ridges and onto both soft dorsal and anal fins. Pelvic axillary scale present and well developed (fig. 23C). Interpelvic scale series present, terminal scale somewhat pointed distally. Lateral-line scales number 36–39 (mode 38). Chest scales noticeably reduced in size and embedded. Belly scales markedly reduced in size compared to chest scales, those along ventral midline smallest and very embedded (such that the belly appears asquamate). Multiple rows of scales, markedly reduced in size, extend on flanks from chest (and continue posteriorly dorsal to pelvic fins and anus) to about anal-fin origin (fig. 23C). These scales of reduced size comprise a deep patch of several rows that is easy to visualize in lateral view. Four or five rows (sometimes also a partial sixth row, e.g., holotype with a single sixth-row scale) of scales on cheek. Opercle and subopercle scaled. Interopercle fully scaled posteriorly, asquamate anteriorly. Preopercle asquamate. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly 2/3 to 3/4 length of fin on dorsal and ventral lobes, and about 1/3 length of fin medially.

Dorsal with XV–XVII spines, 13 or 14 soft rays. Anal with VII–VIII spines, 11 or 12 soft rays. Origin of dorsal fin at about level of, or slightly posterior to, vertical through dorsal margin of pectoral-fin insertion. Caudal fin emarginate, upper and lower lobes rounded. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and

anal fins slightly produced and rounded. Lobes extend well beyond origin of caudal fin. Adducted pelvic fins extend to, or terminate just anterior to, anal-fin origin.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Large, well-developed exoccipital foramina present. Paired anterior gas bladder bullae present, with tough and thickened tunica externa, and anteriormost chambers firmly lodged in exoccipital recesses. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) lacking along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins (structures appear less well developed in *P. nourissati* and *P. tsimoly* than in other species of *Paretroplus*). Nasal bones elongate. Lower pharyngeal jaw (LPJ) with reduced number of interdigitations on ventral suture and indentation on ventral face of posterior horns. Interdigitations along ventral suture of LPJ shallow and weak. Posterior horns of LPJ narrow, particularly along ventrally projecting ridges, and gap present between left and right fifth ceratobranchial elements, posterior to ventral suture.

COLORATION IN LIFE: Stiassny et al. (2001: 38) present a description of live coloration for both sexually quiescent (nonbreeding) and parental (breeding) adults. In addition, de Rham and Nourissat (2004: 125, 127) present several photographs of live aquarium specimens. Body ground coloration pale beige to orangish or reddish brown (nonbreeding, sexually quiescent individuals) to bright yellow, yellowish orange, or bright red (breeding, sexually active individuals), with series of six or seven vertical dark gray to blackish bars extending from the dorsoposterior margin of opercle to caudal peduncle and continuous from dorsum to ventrum. Posteriormost five (or four, as bar on caudal peduncle sometimes pale) bars on the flank are strongly pigmented and more or less equally prominent (Stiassny et al., 2001: fig. 10; de Rham and Nourissat, 2004: 125). Lips, lower cheek, gular region, and belly dark grayish blue, dark purplish gray, or bluish black. Unpaired fins and pelvic fins grayish brown to reddish brown with red margins (nonbreeding), or charcoal with vivid red margins to more or less uniform bright red (breeding). Pelvic fins with white leading edge. Pectoral fins reddish gray, golden brown, or bright red. Grayish to dark gray triangular patch generally visible in pectoral-fin axil.

COLORATION IN PRESERVATIVE: Base body coloration gray to grayish brown. Generally with an overall speckled or blotchy appearance (figs. 51–52). Scale margins generally light gray on flanks, except ventrally where margins sometimes edged in dark brown. Six or seven darker gray to blackish vertical bars present on flanks. In specimens with six lateral bars, first bar at posterior margin of head and next bar in series are coalesced. Two midlaterally located bars, which represent the second and third or third and fourth bars in series, and those on posterior flank relatively strongly pigmented and about equally prominent (fig. 51). Bars on anterior flank quite faint. Body somewhat darker overall dorsally. Dark gray to blackish triangular patch present in pectoral-fin axil (faint in some specimens). Lateral line canals lined with melanophores in some specimens. Head, chest, and belly brownish gray. Snout, lacrimal, and interorbital region brownish gray to dark purplish gray. Lips, lower cheek, gular region, and belly dark charcoal gray to dark bluish gray or purplish gray in some specimens and light grayish brown to gray in others. Unpaired fins gray, grayish black, or black proximal to body, and light gray distally. Dorsal and anal fins sometimes black along margins. Pectoral fins medium gray proximal to body and light gray distally, or uniform gray. Pelvic fins gray proximal to body and charcoal gray distally, or uniform dark gray. Leading edge of pelvic fins whitish to light gray. Lateral barring more prominent in juveniles than adults. In juveniles the entire series of lateral bars is strongly pigmented.

DISTRIBUTION AND HABITATS: The type series of *P. tsimoly* was collected from the Ankalimilotrabe (= Kalamilotra or Kamilo-

tra) River, a tributary of the Betsiboka River, at the town of the same name and just upstream from where it is crossed by the main highway between Majunga (= Mahajanga) and the capital, Antananarivo (Stiassny et al., 2001; de Rham and Nourissat, 2004), approximately 43 km to the northwest of Maevatanana (fig. 48). The Akalimilotrabe River is connected to the Betsiboka River by a series of two floodplain lakes (Stiassny et al., 2001). The substrate at the type locality is rocky, interspersed with patches of gravel and small stones, with numerous rocky outcrops creating a series of pools (also see Stiassny et al., 2001: 39; de Rham and Nourissat, 2004: 124–127). Given that the type locality is at the crossing of the major highway to the north of Madagascar from the capital, Antananarivo, it is surprising that the species was not discovered until the late 1990s. In the original description of this species, Stiassny et al. (2001: 39) note that although no specimens were collected, *P. tsimoly* was also observed in another north bank tributary of the Betsiboka River, the Boinakely River, about 33 km to the northwest of Maevatanana, where it is crossed by the major north-south highway, RN-4. De Rham and Nourissat (2004: 124) mention another population of *P. tsimoly* located in a lake (no name provided) three hours walk to the east of the Kalamilotra River. As far as I can determine, no specimens from this population were preserved.

Subsequent to the description of *P. tsimoly*, de Rham and Nourissat (2004) collected very similar specimens in the upper reaches of the Kamoro River, a tributary of the extensive Betsiboka basin, near the village of Antsalahina, and which they refer to as *Tsimoly* (fig. 48). The upper Kamoro specimens share the characteristic enlarged and lobed lips and dark grayish-blue to bluish-black lips, lower cheek, belly, and gular region with topotypic *P. tsimoly*. Although de Rham and Nourissat (2004: 126) report that, in life, specimens from the upper Kamoro differ slightly in pigmentation pattern and coloration from topotypic *P. tsimoly*, in preservative specimens from these two populations are indistinguishable. Moreover, I am unable to find any anatomical differences to suggest that the Kamoro River population is a distinct species from topotypic *P. tsimoly*.

Interestingly, there appears to be hydrological evidence to support the hypothesis that the Kalamilotra and Kamoro populations are conspecific, as well as to explain species boundaries within Clade F. *Paretroplus lamenabe*, the sister species to the clade comprising *P. nourissati* and *P. tsimoly*, is known only from the lower reaches of the Mahajamba River, near the town of Androka, a locality well downstream from any connection with the Kamoro River (fig. 48). The Mahajamba is the next major basin to the north of the Betsiboka. As noted by Aldegheri (1972), the Mahajamba River is captured by the Kamoro River, a tributary of the Betsiboka, east of Tsaramandroso and near Morafeno, such that the upper 153 km of the Mahajamba flows almost entirely into the Betsiboka basin, whereas the distance from the capture zone to the mouth of the Mahajamba is 145 km. Capture of the upper Mahajamba by the Kamoro occurs well upstream of the range of *P. lamenabe*. Aldegheri (1972: 276) further notes that in periods of low water all of the upper Mahajamba's water goes to the Kamoro, and from this point to the sea, the only water the lower Mahajamba receives is from its small tributaries. Thus, the lower reaches of the Mahajamba are effectively isolated from the Kamoro and Betsiboka basins.

Given the isolation of the lower Mahajamba from both the upper Kamoro and Betsiboka basins, it is not hard to imagine that populations of *Paretroplus tsimoly* in the upper Kamoro and the Kalamilotra (= Ankalimilotrabe) rivers, both tributaries of the Betsiboka River, would be conspecific, whereas a distinct species, *P. lamenabe*, is present in the more or less isolated lower Mahajamba River. Somewhat surprising, however, is the fact that *P. tsimoly* is recovered as the sister taxon to *P. nourissati*, endemic to the Sofia basin located to the north of the Mahajamba, instead of *P. lamenabe*, which occurs in the adjacent basin to the north. Nevertheless, during exceptionally rainy years, the floodplains of the Mahavavy du Sud, Betsiboka, Kamoro, Mahajamba, and Sofia rivers are often contiguous (P. Loiselle in Courtney et al.,

2004), which in part may explain the close relationship between Betsiboka and Sofia endemics.

The conservation status of *P. tsimoly* appears to be stable. De Rham and Nourissat (2004: 126) report that at least in the upper Kamoro River, *P. tsimoly* was relatively abundant when they visited the region in 2001 (and J.-C. Nourissat in 2003). However, judging from the small number of specimens collected from the type locality since the species was discovered in 1996, it would seem that the species is not abundant in the Kalamilotra River. I had briefly fished the Kalamilotra near the type locality in 1994 and did not collect any native cichlids.

LOCAL NAME: *Tsimoly*, which is pronounced "see-MOOL".

ETYMOLOGY: The Malagasy name of this species in the local Sakalava dialect is *tsimoly*.

RELATIONSHIPS AND DISCUSSION: Based on the simultaneous analysis of morphological features and nucleotide characters, *P. tsimoly* is recovered as a member of Clade F and as the sister taxon to *P. nourissati* (fig. 1). Clade F is diagnosed by two unambiguously optimized morphological transformations, the first of which is unique and unreversed: the presence of two prominent and converging midlateral bars (several fainter bars are also present on the flanks) (figs. 51–52) and elongate nasal bones. *Paretroplus damii* is recovered as the sister taxon to Clade F. Clade E, comprising *P. damii*, *P. tsimoly*, *P. nourissati*, and *P. lamenabe*, is united by five unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1).

In addition to the characteristically pigmented and hypertrophied, lobed bluish-gray to bluish-black (in life) or dark bluish-gray (in preservation) lips, a number of additional features serve to distinguish *P. tsimoly* from congeners. *Paretroplus tsimoly* is further distinguished from other members of Clade F, *P. lamenabe* and *P. nourissati,* by a lateral pigmentation pattern in which the posteriormost four or five bars on the flanks are strongly pigmented and about equally prominent (vs. only central two bars, representing the second and third or third and fourth bars in series, strongly pigmented in *P. lamenabe* and *P. nourissati*), and by an overall speckled or blotchy lateral pigmentation pattern (vs. uniform base coloration).

Additionally, *P. tsimoly* can be distinguished from *P. lamenabe* by a shallower body (41.1%–46.8% vs. 47.0%–54.3% in *P. lamenabe*) and by shorter pelvic fins that do not extend to anal-fin origin when adducted, and from *P. nourissati* by posterior extensions of the soft dorsal and anal fins that extend well beyond caudal-fin origin even in the smallest specimen examined (89.7 mm SL) in which the fins were not damaged (vs. posterior fin margins either not reaching, or, in some large specimens, extending to or rarely slightly beyond caudal-fin origin in *P. nourissati*). *Paretroplus tsimoly* and *P. nourissati* can generally be distinguished from *P. lamenabe* by a lower tooth count in the upper jaw (12–14 in *P. tsimoly* and 13–16 in *P. nourissati* and respectively, vs. 15–18 in *P. lamenabe*), and by less extensive squamation extending onto the membranes of the soft dorsal and anal fins.

As in other members of Clade F, *P. tsimoly* exhibits both a reduced number of interdigitations (which are shallow and weak) on the ventral suture and an indentation on the ventral face of the posterior horns of the LPJ. In addition, members of Clade F are united by narrow posterior horns of the LPJ, especially along the ventral ridges, and, posterior to the ventral suture, by a narrow gap between left and right fifth ceratobranchial elements.

Paretroplus damii and its sister taxon, Clade F, comprise Clade E. Members of Clade E are unique among *Paretroplus* in a number of features of scale morphology and squamation pattern, including: the posterior field of the flank scales is unossified and thin (fig. 23C), multiple rows of scales extend onto the membranes of both the soft dorsal and anal fins, the chest scales are markedly reduced in size and highly embedded, and multiple rows of scales of reduced size extend from the chest, dorsal to the pelvic fins and anus, to approximately anal-fin origin (fig. 23C). Members of Clade F can be distinguished from congeners, including *P. damii*, by exceedingly reduced (in size) and strongly embedded chest and belly scales,

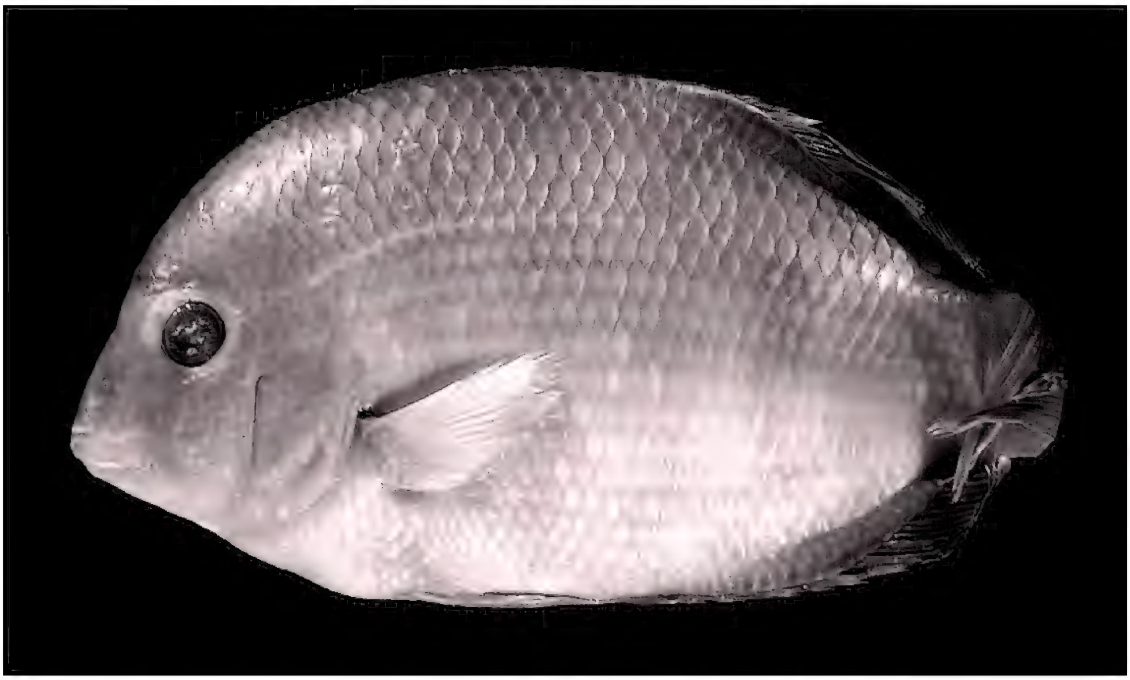


Fig. 53. *Paretroplus dambabe*, holotype, UMMZ 238724, 169.4 mm SL; northwestern Madagascar: Mahajanga Province: south of Mitsinjo: Mahavavy (du sud) drainage basin: Lake Kinkony.

such that the ventral chest and belly appear asquamate.

Paretroplus dambabe Sparks, 2002
Figures 35, 53–54; plate 1J; table 11

Paretroplus petiti: Kiener, 1963 (in part); Kiener and Thérézien, 1963; Kiener and Maugé, 1966 (in part); Stiassny et al., 2001.

Paretroplus cf. *petiti*: de Rham and Nourissat, 2002.

Paretroplus nov. sp. "dambabe": Sparks and Stiassny, 2003: table 9.1.

HOLOTYPE: UMMZ 238724, adult male, 169.4 mm SL; northwestern Madagascar: Majunga (Mahajanga) Province: south of Mitsinjo: Mahavavy (du sud) drainage basin: Lake Kinkony: 16°05′37.7″S, 45°51′37.4″E; JSS 94-15; J. S. Sparks, K. J. Riseng, and local Malagasy guides, 14–16 July 1994.

PARATYPES: UMMZ 199406, 3 ex., 67.0–113.0 mm SL; ex. MNHN 60579; Madagascar. AMNH 232398, 10 ex., 61.0–170.0 mm SL; data as for holotype. UMMZ 235024, 29 ex., 40.2–225.0 mm SL, 3 ex. C&S; data as for holotype.

ADDITIONAL NONTYPE MATERIAL EXAMINED: All from Madagascar, Majunga (Mahajanga) Province, Mahavavy (du sud) drainage basin, Lake Kinkony: AMNH 11707, 2 ex., 137.5–153.5 mm SL; Archbold Expedition: A. L. Rand and P. A. Dumont, III-1931. AMNH 97371, 1 ex., 77.4 mm SL; P. V. Loiselle and local fishermen, 27-VI-1993. MHNG 2537.48, 6 ex., 83.6–166.4 mm SL; Mitsinjo; P. de Rham and J.-C. Nourissat, 23-X-1992. MHNG 2537.72, 5 ex., 1 ex C&S; 74.3–89.0 mm SL; Mitsinjo; P. de Rham and J.-C. Nourissat, XI-1991. MNHN 1960-0579, 3 ex., 125.5–179.9 mm SL; A. Kiener. MNHN 1962-0239, 2 ex., 23.3–24.6 mm SL; A. Kiener. MNHN 1965-0316, 2 ex., 64.2–129.3 mm SL; G. Petit. MNHN 1996-123, 1 ex., 105.2 mm SL; J.-C. Nourissat and P. de Rham.

DIAGNOSIS: A member of the deep-bodied clade of *Paretroplus* (Clade I) and distinguished from congeners, in preservative, by pale yellow to golden body coloration in combination with a series of six or seven faint to barely discernable (particularly in

Fig. 54. *Paretroplus dambabe*, AMNH 97371, 77.6 mm SL; northwestern Madagascar: Mahajanga Province: Mahavavy (du sud) drainage basin: Lake Kinkony. Illustrating mottled pigmentation pattern characteristic of juveniles and subadults.

adults) vertical, dark-olive bars on the flank, and in the possession of uniform gray or charcoal-gray unpaired fins. In life, *P. dambabe* is unique among congeners in the possession of a grayish to bluish-green base coloration, which is accompanied by a highly variable amount of bright red pigmentation on the flank, particularly below the upper branch of the lateral line. *Paretroplus dambabe* is further distinguished from *P. petiti*, a species with which it has been erroneously associated for decades, by overall coloration (light yellowish olive vs. dark brown), brownish spotting (reddish in life) on the flanks in preservative, particularly anteriorly and below the lateral midline, and a shallower body (mean 52.8% [ranges from 48.3%–57.1%] vs. 57.9% SL).

DESCRIPTION: Morphometric and meristic data presented in table 11. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 53–54. A deep-bodied, laterally compressed *Paretroplus* belonging to Clade I, discussed by Sparks and Reinthal (1999) and Sparks and Smith (2004), and comprising all deep-bodied and essentially disk-shaped members of *Paretroplus* (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, *P. petiti*, and *P. polyactis*) (fig. 1). Comparatively a large *Paretroplus*, frequently exceeding 200 mm SL, and reportedly attaining 400 mm TL (Kiener, 1963), although large specimens now rare (see below). Head blunt and steeply sloping in lateral view. Predorsal profile rounded and convex, especially pronounced in larger individuals. Caudal peduncle short, deep, and laterally compressed. Females smaller than males, but no additional sexually dimorphic characters apparent.

Total vertebral count 31–33 (mode 32), with formulae of: 14 + 18, 14 + 19, 15 + 16, 15 + 17, and 15 + 18, precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, and other teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw usually number six to eight on each side, rarely five. Teeth in lower

TABLE 11
Morphometric and meristic data for *Paretroplus dambabe*. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

		P. dambabe			
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	20	169.4	40.7–186.8	115.9	
Percentage of SL					
Head width (max.)	20	17.4	16.0–17.5	16.7	0.49
Head length	20	30.4	27.8–33.2	30.7	1.51
Body depth	20	57.0	48.3–57.1	52.8	2.92
Caudal peduncle length	20	6.2	5.1–8.6	6.4	0.66
Caudal peduncle width	20	5.9	2.7–5.9	4.5	0.82
Caudal peduncle depth	20	17.7	15.1–18.2	16.7	0.88
Pectoral-fin length	20	22.3	20.1–23.4	21.6	1.05
Pelvic-fin length	20	23.6	22.1–26.3	23.5	0.96
Last dorsal spine length	19	14.5	13.3–16.9	15.4	0.97
Percentage of HL					
Snout length	20	48.5	31.9–48.9	43.7	4.64
Orbit diameter	20	26.4	26.4–39.3	31.3	3.74
Upper jaw length	20	30.1	25.7–31.3	28.3	1.59
Lower jaw length	20	35.7	29.9–36.3	34.1	1.79
Interorbital width	20	36.5	28.2–41.7	35.5	3.07
Preorbital depth	20	34.4	22.2–37.6	31.4	4.10
Caudal peduncle length/width	20	1.1	1.1–2.0	1.5	0.26
Caudal peduncle length/depth	20	0.4	0.3–0.5	0.4	0.04
Scales in lateral line	20	36 (10), 37 (7) (H), 38 (3)			
Scales: lateral line to dorsal fin	20	6 (3), 6.5 (1), 7 (16) (H)			
Gill rakers (lower limb 1st arch)	20	9 (13), 10 (7) (H)			
Vertebrae (precaudal + caudal)	30	14 + 18 = 32 (5), 14 + 19 = 33 (1), 15 + 16 = 31 (1), 15 + 17 = 32 (17) (H), 15 + 18 = 33 (6)			
Dorsal fin	30	XVI 18 (3), XVI 19 (1), XVII 17 (6), XVII 18 (15) (H), XVII 19 (4), XVIII 17 (1)			
Anal fin	30	VIII 14 (3), VIII 15 (2), IX 13 (9), IX 14 (11) (H), IX 15 (2), X 13 (2), X 14 (1)			

jaw number three to five on each side. Lower-jaw teeth irregularly spaced and sized.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially (fig. 14B). LPJ well sutured, with numerous interdigitating sutures on posteroventral margin. Five to seven robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Tooth plates not confluent with outer-row gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially (fig. 11D). Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three to four rows (fig. 11D).

Nine or 10 triangular, somewhat elongate, gill rakers arrayed along lower limb of first gill arch. Rakers edentate in small individuals (<100 mm SL) and weakly denticulate dorsomedially in larger specimens. All other lower-limb rakers (i.e., those on gill arches 2–4) short and strongly denticulate dorsally.

Epibranchial rakers on first gill arch elongate, numbering 8–10.

Body covered with large, regularly imbricate, cycloid scales. Well-developed ridges of scales (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from both spiny and soft portions of dorsal and anal fins. Pelvic axillary scale present and well developed. Lateral-line scales number 36–38 (mode 36). Chest scales only slightly smaller than lateral body scales and weakly embedded. Belly scales along ventral midline markedly reduced in size and embedded, much smaller than lateral body and chest scales. Four to six rows of scales on cheek. Opercle, subopercle, and interopercle scaled. Snout, lacrimal, and anterior portion of interorbital region asquamate. Preopercle scaled dorsally along shaft, and ventrally only along anterior margin. Scales on caudal fin reduced in size and extending posteriorly 2/3 to 3/4 length of fin on dorsal and ventral lobes, and 1/4 to 1/3 length of fin medially.

Dorsal with XVI–XVIII spines, 17–19 soft rays. Anal with VIII–X spines, 13–15 soft rays. Origin of dorsal fin slightly anterior of vertical through pectoral-fin insertion. Caudal fin emarginate and crescent shaped, trailing margins of upper and lower lobes produced, particularly in larger individuals. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins produced and pointed in larger specimens. Pelvic fins extending just to anal-fin origin in smaller specimens, and well beyond origin in larger individuals.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital foramina present (fig. 10B). Paired anterior gas bladder bullae with tough and thickened tunica externa, and anteriormost chambers firmly lodged in exoccipital recesses. Expansive, wide and rounded excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital (fig. 10B). Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977) (fig. 10B). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

Coloration in Life: Ground coloration grayish, grayish pink, or bluish green (see de Rham and Nourissat, 2004: 95, 97). Body generally darker dorsally, but sometimes uniform in coloration. Alternating light and dark horizontal striping pattern evident on flank. Six or seven broad, vertical dark olive bars extending from anterior region of trunk to caudal peduncle; bars very obvious in juveniles, becoming less conspicuous to nearly indistinguishable in large adults. A variable amount of vivid red pigmentation (= spotting) present on flanks, particularly below upper branch of lateral line. Some individuals with each flank scale outlined in red, whereas in others, red pigmentation restricted to region below upper branch of lateral line. Nape and region below anterior spinous dorsal golden in juveniles. Black interorbital bar present in adults, and dark golden in juveniles. Dorsal and anal fins uniformly black proximal to base. Soft dorsal and anal fins with white distal margin. Caudal fin orangish anteriorly, black on median portion of fin, and with white terminal band. Pelvic fin black with white leading edge. Pectoral fin reddish orange proximal to base, white distally. Pigmentation pattern of young fish (<30 mm SL) blotchy and mottled (see juvenile *P. petiti* [now *P. dambabe*] illustrated by Kiener, 1963: Pl. 16).

Coloration in Preservative: Ground coloration pale yellowish olive or light tan. Six or seven weak to barely discernable vertical, dark-olive bars on flank (fig. 53). Barring more conspicuous in subadults (<150 mm SL) than adults (Sparks, 2002a: fig. 3), and becoming obscure to barely visible in large adults (fig. 53). Pigmentation pattern of juveniles blotchy and mottled overall (fig. 54). Reddish coloration on anterior flank faded and appearing brownish in preservative. Alternating light and dark horizontal striping pattern obvious on flank. Unpaired fins and pelvic fins uniform charcoal gray. Pectoral fins olive proximal to base and more or less hyaline distally. Anterior interorbital region and snout light gray.

VISCERA AND DIET: Contents of gut in all individuals examined comprised entirely of crushed gastropods.

DISTRIBUTION AND HABITATS: Although *Paretroplus dambabe* is reported to have a slightly wider geographic range within the Mahavavy du Sud basin, preserved specimens are only available from Lake Kinkony, a large, shallow floodplain lake located to the southwest of Majunga in the northwestern part of the island (fig. 35). The species is also reported to occur in two smaller satellite lakes near the village of Antongomena (de Rham and Nourissat, 2004), and in the Mahavavy du Sud River (P. Loiselle, personal commun.). I have collected and examined material only from Lake Kinkony proper, and cannot confirm these additional localities. Lake Kinkony is a large (second largest lake in Madagascar, ca. 14,000 hectares), extremely shallow and turbid, oligotrophic floodplain lake characteristic of basins in northwestern Madagascar (Kiener, 1963). Similar lakes in northwestern Madagascar include lakes Andrapongy and Sarodrano. Several euryhaline and invasive marine species, including anguillids, carangids, *Scatophagus*, and *Chanos*, also inhabit the lake. The Lake Kinkony basin is moderately to highly disturbed and degraded. A substantial portion of the basin has been converted for rice cultivation and for grazing of livestock, and little original riparian vegetation remains in the basin.

According to local fishermen questioned in the mid-1990s, the species had suffered a dramatic decline in abundance in the preceding decade. Lake Kinkony is subjected to severe fishing pressure, especially from seasonal migrant fishermen who supply markets in the capital, Antananarivo. Regrettably, de Rham and Nourissat (2004: 93–96) report that *P. dambabe* is most certainly extinct in Lake Kinkony, but that in 1997 populations of *P. dambabe* were also discovered in two smaller satellite lakes, Andranobe and Lac de la Digue, situated near the town of Antongomena. Although they were unable to collect specimens in Lake Andranobe, which was under heavy fishing pressure, Lac de la Digue, an artificial lake used to store water for rice irrigation, still harbored a population of *P. dambabe* (de Rham and Nourissat, 2004). Another member of *Paretroplus*, *P. kieneri*, also occurred in Lake Kinkony, which is the type locality for this species, but is also now reported to be extinct in the basin. In the mid-1990s, *P. kieneri* was extremely rare in Lake Kinkony, whereas a few specimens of *P. dambabe* could still be collected, but with substantial effort.

LOCAL NAME: *Kotso*, *Damba*.

ETYMOLOGY: *Dambabe* (pronounced "dambah bay") is a compound Malagasy word that translates as "large" or "big" (= *be*) *damba,* in reference to the large size attained by this species relative to most other members of the genus. *Damba* is the Malagasy word used to refer to a number of species of *Paretroplus* throughout northwestern Madagascar. According to de Rham and Nourissat (2004: 88), *damba* was the name originally used by the Merina fish traders.

RELATIONSHIPS AND DISCUSSION: *Paretroplus dambabe* is a member of Clade I, comprising all the deep-bodied and essentially disk-shaped members of *Paretroplus* (*P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, *P. petiti*, and *P. polyactis*), which is supported by three unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1). All members of this clade are morphologically similar apart from pigmentation pattern and coloration.

In the combined analysis of morphological features and nucleotide characters, *P. dambabe* is recovered in an unresolved polytomy with all other deep-bodied species of *Paretroplus* that have distributions confined to western basins (fig. 1: Clade J). Monophyly of Clade J, comprising *P. dambabe*, *P. maculatus*, *P. maromandia*, *P. menarambo*, and *P. petiti*, is supported by two unambiguously optimized morphological features, the second of which is unique and unreversed: the presence of a blunt snout with a steeply sloping profile in lateral view and a distinctive lateral pigmentation pattern comprising alternating horizontal light and dark stripes (fig. 53). A lack of resolution within Clade J is due to the fact the *P. petiti* (known only from the formalin-fixed holotype) is included on the basis of morphological features only, which are insufficient for resolving relation-

ships within this morphologically conservative clade. In a combined analysis of morphological features and nucleotide characters that specifically excluded *P. petiti*, *P. dambabe* is recovered as the sister taxon to *P. maculatus* (fig. 2), a result also obtained on the basis of nucleotide characters only (Sparks, 2004a; Sparks and Smith, 2004).

Although *P. dambabe* was only recently described (Sparks, 2002a), since at least the early 1960s individuals of this species collected from Lac Kinkony have erroneously been referred to *P. petiti* (e.g., Kiener, 1963; Kiener and Thérézien, 1963; Kiener and Maugé, 1966). Based on results presented by Sparks (2002a), all specimens previously assigned to *P. petiti* that were collected in Lac Kinkony are determined instead to be members of *P. dambabe*. *Paretroplus dambabe* is readily distinguished from *P. petiti* in preservative by overall coloration (light yellowish olive vs. dark brown), brownish spotting (reddish in life) on the flanks, particularly anteriorly and below the lateral midline, and a shallower body (mean 52.8% [ranges from 48.3%–57.1%] vs. 57.9% SL). *Paretroplus petiti* is, therefore, currently only known from the holotype described by Pellegrin (1929).

As discussed by Sparks (2002a), there has been some confusion and misunderstanding regarding the type locality of *P. petiti* Pellegrin, 1929, which in the original description is listed as the Maintimaso River in the province of Mahajunga, northwestern Madagascar. As far as I can determine, the type specimen of *P. petiti* (MNHN 1928-282) was collected from the Maintimaso River, a tributary of the westward flowing Betsiboka River, near the town of Maintimaso (16°10′60″S, 46°43′00″E), which is situated about 37 km southeast of Majunga (= Mahajunga) (see fig. 35). The MNHN database, however, lists the collection locality of this specimen as "Ambila". No town with this spelling could be located in the vicinity of Majunga, although the town of Ambilo is located near the Betsiboka River, 35 km south of Majunga and to the northwest of Maintimaso. In addition, in the jar with the type specimen at the MNHN (Paris) was an old tag with the species name and also including the word "Ambanja," a town located several hundred km to the north of Maintimaso and Mahajunga. No additional information with regard to either the Ambila or Ambanja localities could be located. As with many other fish species described from Madagascar in the latter part of the 19th century through the first half of the 20th century, collection localities are frequently ambiguous and questionable (Sparks, 2002a). Nevertheless, it is clear from the information that is available that the type specimen of *P. petiti* was not collected from the Mahavavy du Sud drainage basin, to which *P. dambabe* is endemic, but instead was obtained from a tributary of the Betsiboka River, one of Madagascar's largest drainage basins (fig. 35).

As noted by Sparks (2002a), the holotype of *P. petiti*, a juvenile, is considerably deeper bodied than *P. dambabe* of similar standard length, and is deeper bodied than any individual of *P. dambabe* examined, whereas it is similar in body depth to specimens of *P. menarambo* of similar standard length (Sparks, 2002a: fig. 8). The holotype and only known specimen of *P. petiti* is remarkably well preserved and similar in body shape and pigmentation pattern, in preservation, to *P. menarambo*, a species restricted to floodplain lakes of the Sofia basin, northwestern Madagascar (cf. figs. 34 and 42–43). Both species are dark brown, with a pattern of alternating horizontal light and dark stripes on the flank. Although other deep-bodied members of *Paretroplus* (Clade J) possess this characteristic horizontal striping pattern, none other than *P. petiti* and *P. menarambo* are dark brown with no additional lateral markings apart from a faint vertical barring pattern in *P. menarambo*. Pellegrin (1929) commented on the horizontal striping pattern in *P. petiti*, but he did not mention any additional distinctive markings. *Paretroplus menarambo* is characterized in life by bright red terminal margins to the unpaired fins, whereas coloration in life for *P. petiti* is not known. Based on these observations, Sparks (2002a) hypothesized that *P. petiti* and *P. menarambo* might be conspecific, but deferred judgment until more material from the region of the putative type locality of *P. petiti* became available.

Fig. 55. *Paretroplus gymnopreopercularis*, holotype, UMMZ 247710, 132.8 mm SL; northeastern Madagascar: Mahajanga Province: northeast of town of Mandritsara: Amboaboa River.

Paretroplus gymnopreopercularis, new species
Figures 38, 55–56, 57B; plate 1K; table 12

Paretroplus nov. sp. "sofia": Sparks and Stiassny, 2003: table 9.1.

Paretroplus kieneri "Amboaboa": Sparks and Smith, 2004: fig. 1, table 1.

Paretroplus kieneri "Mangarahara and Ambomboa [sic] rivers": de Rham and Nourissat, 2004: 111–113.

HOLOTYPE: UMMZ 247710 (ex. UMMZ 239532), 132.8 mm SL; northeastern Madagascar: Mahajanga Province: northeast of town of Mandritsara: Amboaboa River, near confluence with Mangarahara River: 15°50′1.0″S, 48°42′51.0″E, altitude 210.3 m; JSS 96-25; J. S. Sparks and K. J. Riseng, 10-VII-1996.

PARATYPES: AMNH 97365, 4 ex., 1 ex. C&S, 92.0–102.0 mm SL; northeastern Madagascar: Mahajunga Province: west of Mandritsara: Sofia River drainage: Ambomboa [sic] River; P. V. Loiselle, R. Morris, B. Vesta, and local villagers, 22-VI-1993. UMMZ 239531, 6 ex., 80.6–146.7 mm SL: northeastern Madagascar: Mahajanga Province: northeast of town of Mandritsara: Amboaboa River, near where it flows into Mangarahara River: 15°50′1.0″S, 48°42′52.0″E; JSS 94-18; J. S. Sparks and K. J. Riseng, 24-VII-1994. UMMZ 239532, 16 ex., 3 ex. C&S; 73.0–138.1 mm SL; data as for holotype. UMMZ 239533, 2 ex., 91.0–93.0 mm SL; northeastern Madagascar: Mahajanga Province: northeast of town of Mandritsara: Mangarahara River, just downstream from confluence with Amboaboa River: 15°50′1.0″S, 48°42′51.0″E, altitude 210.3 m; JSS 96-26; J. S. Sparks and K. J. Riseng, 11-VIII-1996. UMMZ 239546, 2 ex., 76.0–90.0 mm SL; northeastern Madagascar: Mahajanga Province: northeast of town of Mandritsara: Amboaboa River, near where it flows into Mangarahara River: 15°50′2.0″S, 48°42′52.0″E; JSS 94-53; J. S. Sparks and K. J. Riseng, 14-XI-1994

DIAGNOSIS: An elongate *Paretroplus* distinguished from all congeners except *P. kieneri* by the presence of a blotchy and mottled (orangish-brown to golden-brown) pigmentation pattern, the absence of both vertical bars and a horizontal striping pattern on the flanks, and the presence of a fleshy snout that extends both rostral to the lips and also ventrally to cover a portion of the upper lip. *Paretroplus gymnopreopercularis* is distin-

Fig. 56. *Paretroplus gymnopreopercularis*, paratype, UMMZ 239532, 72.5 mm SL, illustrating mottled juvenile pigmentation pattern. Locality data as for holotype.

guished from *P. kieneri* by the presence of an asquamate preopercle (vs. fully scaled or scaled except along the ventral margin) and a blunt, strongly convex predorsal profile (vs. pointed). In *P. gymnopreopercularis* the second lacrimal plate is excluded from the orbit margin owing to contact of the first lacrimal plate and the third infraorbital bone in series (vs. narrow prong of the second lacrimal plate extending into the orbit margin in *P. kieneri*). In addition, *P. kieneri* is conspicuously blotchy, mottled, and speckled, and generally exhibits dark gray coloration (e.g., frequently on the head and fins). In contrast, *P. gymnopreopercularis* is characterized by a weakly mottled and for the most part uniform chain-link pigmentation pattern, owing to darkly pigmented scale margins, and is never dark gray, but orangish brown to golden brown overall.

DESCRIPTION: Morphometric and meristic data presented in table 12. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 55–56. An elongate, shallow bodied and comparatively small *Paretroplus* belonging to Clade H (fig. 1) that reaches about 150 mm SL. Comparative data for its sister taxon, *P. kieneri*, presented in table 5. Body laterally compressed. Head blunt and snout moderately to strongly convex and rounded, lending the fish a beaked appearance. Predorsal profile markedly curved. Dorsal body outline moderately curved, ventral outline mostly straight, except posteriorly. Caudal peduncle somewhat short, moderately deep, and laterally compressed, yet much longer and shallower than members of the deep-bodied clade (Clade I). No sexually dimorphic characters readily apparent.

Total vertebral count 32 to 34 (mode 33), with formulae of: 14 + 18, 14 + 19, 15 + 18, and 15 + 19, precaudal and caudal vertebrae, respectively.

Jaws isognathous. Single row of spatulate unicuspid teeth in both upper and lower jaws (fig. 4D). Teeth laterally expanded, flattened at crown, and procumbently implanted. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, other teeth laterally graded in size. Lower-jaw teeth at symphysis not enlarged, but somewhat reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth (fig. 4D). Teeth in upper jaw number 4 or 5 on each side, and total 8–10. Teeth in lower jaw number four or five on each side, and total nine. Upper and

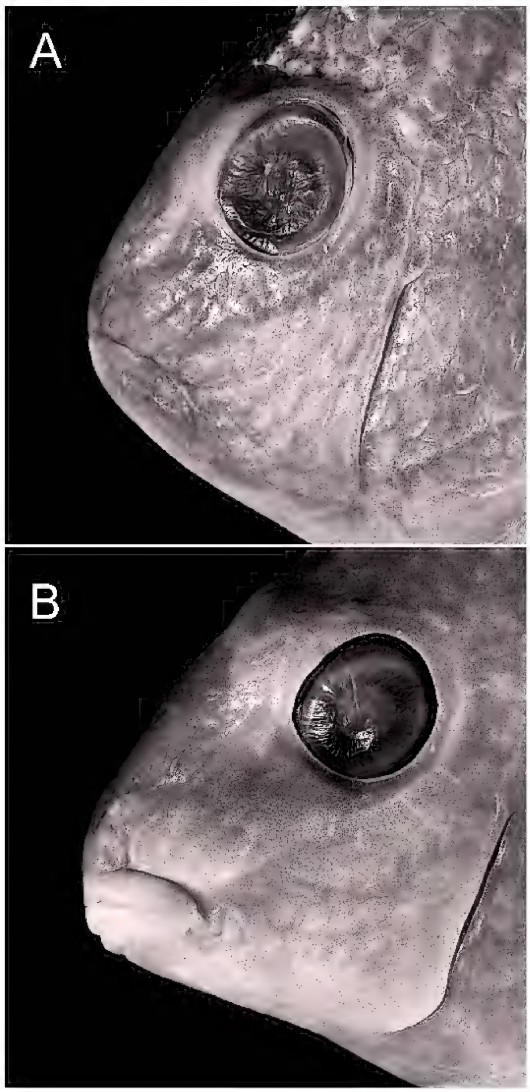


Fig. 57. Left lateral view of the suspensorium illustrating squamation pattern on preopercle: **A,** *Paretroplus kieneri*, AMNH 238560, 124.1 mm SL. **B,** *Paretroplus gymnopreopercularis*, paratype, UMMZ 239531, 146.6 mm SL.

lower-jaw teeth generally widely set. Symphyseal teeth (and sometimes adjacent lateral teeth) in both upper and lower jaws closely set.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchials) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. LPJ well sutured, with numerous interdigitating sutures on posteroventral margin. Five or six robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Tooth plates occasionally become fused. Tooth plates not confluent with outer-row gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates becoming robust medially. Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three rows.

Nine or 10 triangular (mode 9), somewhat elongate gill rakers arrayed along lower limb of first gill arch. Some rakers weakly to moderately denticulate dorsomedially. All other lower-limb rakers (i.e., those on gill arches 2–4) short and strongly denticulate dorsally, and essentially spherical in shape. Teeth on rakers of gill arches 2–4 as long or longer than raker itself. Epibranchial rakers on first gill arch elongate, numbering six to eight.

Body covered with large, regularly imbricate, cycloid scales. Well-developed scale ridges (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from spiny dorsal and anal fins, but becoming weakly attached to both soft dorsal and anal. Pelvic axillary scale present and well developed. Lateral-line scales number 37–39 (mode 38). Interpelvic scale well developed and elongate. Ventral chest scales reduced in size and embedded; those along ventral midline smallest. Three rows of scales on cheek; occasionally an incomplete fourth row present. Opercle, subopercle, and interopercle scaled. Preopercle asquamate (in some specimens scales extend partially over dorsalmost portion of shaft of preopercle). Snout and lacrimal asquamate. Scales on head extend well anterior of a vertical through anterior margin of orbit. Scales on caudal fin reduced in size and extending posteriorly 2/3 to over 3/4 length of fin on dorsal and ventral

TABLE 12

Morphometric and meristic data for *Paretroplus gymnopreopercularis*, new species. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

	P. gymnopreopercularis				
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	20	132.8	73.0–146.7	101.6	
Percentage of SL					
Head width (max.)	20	15.5	14.3–16.6	15.6	0.59
Head length	20	28.3	27.0–29.7	28.3	0.63
Body depth	20	44.1	39.1–45.7	42.4	1.90
Caudal peduncle length	20	9.9	7.4–11.6	10.0	0.96
Caudal peduncle width	20	4.4	4.3–6.2	5.1	0.54
Caudal peduncle depth	20	15.1	13.7–15.3	14.7	0.41
Pectoral-fin length	20	21.8	19.8–22.6	21.3	0.78
Pelvic-fin length	20	21.5	20.1–22.3	21.4	0.56
Last dorsal spine length	6	15.1	14.1–15.7	15.0	0.52
Pre-dorsal length	17	42.2	39.7–43.1	41.3	0.91
Pre-anal length	17	53.7	51.1–55.1	53.0	1.08
Pre-pelvic length	17	35.3	33.2–37.6	35.3	1.12
Percentage of HL					
Snout length	20	45.0	34.8–45.0	40.8	2.46
Orbit diameter	20	27.9	27.9–34.8	30.3	1.81
Upper jaw length	20	27.9	24.7–27.9	26.4	0.99
Lower jaw length	20	30.9	29.5–34.8	31.5	1.42
Interorbital width	20	34.0	30.1–37.3	32.5	1.98
Preorbital depth	20	30.1	20.8–30.6	25.9	2.71
Caudal peduncle length/width	20	2.3	1.6–2.4	2.0	0.24
Caudal peduncle length/depth	20	0.7	0.5–0.8	0.7	0.07
Scales in lateral line	20	37 (4), 38 (9) (H), 39 (7)			
Scales: lateral line to dorsal fin	6	5 (3), 6 (2) (H), 7 (1)			
Gill rakers (lower limb 1st arch)	20	9 (15) (H), 10 (5)			
Vertebrae (precaudal + caudal)	20	14 + 18 = 32 (2), 14 + 19 = 33 (5) (H), 15 + 18 = 33 (12), 15 + 19 = 34 (1)			
Dorsal fin	20	XVII 14 (1), XVII 15 (1), XVIII 13 (5), XVIII 14 (6) (H), XVIII 15 (1), XIX 13 (4), XIX 14 (2)			
Anal fin	20	VIII 12 (1), VIII 13 (1), IX 12 (9) (H), IX 13 (7), X 11 (1), X 12 (1)			

lobes, and about 1/4 to 1/3 length of fin medially.

Dorsal with XVII–XIX spines, 13–15 soft rays. Anal with VIII–X spines, 11–13 soft rays. Origin of dorsal fin slightly posterior of vertical through pectoral-fin insertion. Caudal fin emarginate, trailing margins of upper and lower lobes weakly produced in larger individuals. Pectoral fin broad and rounded at distal margin. Distal margins of soft dorsal and anal fins mildly produced and pointed in larger specimens, and extend slightly beyond origin of caudal fin. Pelvic fins extend slightly beyond anal-fin origin when adducted.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Large, well-developed exoccipital foramina present. Paired anterior gas bladder bullae with tough and thickened tunica externa, and anteriormost chambers firmly lodged in exoccipital recesses. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) along posterior margin of supraoccipital. Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* with-

in Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins.

COLORATION IN LIFE: Base body coloration mildly blotchy and spotted orangish-brown, to golden-brown or dark olive (see de Rham and Nourissat, 2002: 112 [Mangarahara River specimen, center right image], for color photograph). Scale margins generally dark olive to dark brown; scale centers much lighter orangish brown to pale golden brown. Degree of scale margin pigmentation varies considerably over flank, and some scales solid dark golden-brown to dark brown, creating spotted and blotchy chain-link pigmentation pattern characteristic of species. No additional distinctive markings present on head or flanks. No vertical bars present on flanks, even in juvenile specimens. Dorsal fin, anal fin, pectoral fins, and pelvic fins orangish brown to golden brown, and similar to body ground coloration. Dorsal fin with some black pigment distally. Caudal fin golden brown to brown, and rays dark brown to blackish. Juveniles to about 75 mm SL mottled golden brown and appearing camouflaged, owing to large and irregular blotches on flanks (adults become more uniformly pigmented over flank).

COLORATION IN PRESERVATIVE: Body ground coloration golden, orangish brown, or golden brown, with varying amount of darker brown spotting and blotching on flanks (figs. 24D and 55). Scale margins generally darker than centers; this pigmentation pattern more pronounced in some areas, or some scales dark overall, creating spotted and blotchy overall appearance. No other distinctive markings. Body pigmentation generally uniform and not noticeably darker dorsally. Unpaired fins and pectoral fins pale golden brown to light brown. Pelvic fins golden brown to grayish brown. Juveniles to about 75 mm SL mottled golden brown and appearing camouflaged, owing to large and irregular blotches on flanks (adults become more speckled and spotted) (fig. 56).

DISTRIBUTION AND HABITATS: *Paretroplus gymnopreopercularis* has been collected only in the Mangarahara River and its tributary the Amboaboa River, near their confluence, which is located in northeastern Madagascar and near the town of Mandritsara (fig. 38). The Mangarahara is a moderately sized left-bank tributary of the extensive westward flowing Sofia drainage. *Paretroplus gymnopreopercularis* co-occurs in these rivers with *Paretroplus nourissati*. Ichthyological surveys in this remote region of Madagascar have not been extensive and the species could potentially be more widespread in distribution.

The Amboaboa and Mangarahara rivers near the type locality are shallow, clear (low in turbidity), and the current is swift, with many areas of small cascades and riffles. These rivers flow over large areas of exposed bedrock, and the substrate is generally rocky (with many exposed boulders), interspersed with areas of sand. *Paretroplus gymnopreopercularis* appears to be restricted to deeper isolated pools, whereas *P. nourissati* frequents shallow, rocky stretches with a swift current and riffles.

Although neither widespread in distribution nor abundant within its limited range in the Mangarahara or Amboaboa rivers (relative to *P. nourissati*, which is quite common), *P. gymnopreopercularis* would seem to be vulnerable to increased fishing pressure and continued habitat degradation. The Amboaboa River harbors a comparatively species-rich fauna of freshwater fishes for Madagascar, comprising a number of species endemic to the basin (e.g., *Paretroplus nourissati*, *P. gymnopreopercularis*, *Rheocles derhami*, *Sauvagella robusta*, *Ptychochromis insolitus*, and an undescribed species of *Pachypanchax* [P. Loiselle, personal commun.]; also see Ng and Sparks [2003]).

Regrettably, de Rham and Nourissat (2004: 121–123) report that in the late 1990s a dam was constructed, financed by the World Bank, on the Mangarahara River upstream from its confluence with the Amboaboa to permit year-round rice cultivation, which essentially resulted in complete desiccation of the Mangarahara downstream of the dam during the dry season. This has resulted in the extirpation of native fishes for several kilometers downstream from the dam. Although de Rham and Nourissat (2004) were able to collect some specimens in the Amboaboa River during their last visit

in October 1999, they note a sharp decline in abundance for both *Paretroplus nourissati* and the regions only endemic bedotiid rainbowfish, *Rheocles derhami*. Subsequent ichthyological surveys of the Amboaboa River conducted in 2004 and 2006 failed to obtain specimens of *Paretroplus gymnopreopercularis*, *Rheocles derhami*, and *Ptychochromis insolitus* (P. Loiselle, personal commun.).

LOCAL NAMES: *Melemshiska*.

ETYMOLOGY: The specific epithet, *gymnopreopercularis*, refers to the characteristic asquamate (= naked) preopercle in this species.

RELATIONSHIPS AND DISCUSSION: Based on the simultaneous analysis of morphological features and nucleotide characters, *P. gymnopreopercularis* is recovered as a member of Clade H and as the sister taxon to *P. kieneri* (fig. 1). Clade H is supported by a single unambiguously optimized unique and unreversed morphological feature, the presence of a mottled and blotchy overall pigmentation pattern (figs. 24D, 36–37, and 55). This clade in turn is recovered as the sister taxon to Clade I, which comprises all deep-bodied members of the genus (i.e., *P. polyactis*, *P. maculatus*, *P. dambabe*, *P. petiti*, *P. menarambo*, and *P. maromandia*) (fig. 1). In an analysis combining nucleotide characters from both nuclear and mitochondrial genes (J. S. Sparks and W. L. Smith, unpubl. data), *P. gymnopreopercularis* was robustly recovered as the sister taxon to a clade comprising three geographically distinct populations of *P. kieneri*, ranging from the Betsiboka drainage basin and Lake Parinandrina, to the Mahavavy du Sud basin and Lake Kinkony.

Although *P. gymnopreopercularis* and *P. kieneri* are morphologically quite similar, the two species can readily be distinguished by degree of squamation on the preopercle (asquamate in *P. gymnopreopercularis* [fig. 57B] vs. scaled in *P. kieneri* [fig. 57A]) and pigmentation pattern. The pigmentation patterns of both species are characteristically blotchy and mottled compared to other *Paretroplus*; however, that of *P. kieneri* is irregular and generally strongly blotched (figs. 36–37), whereas that of *P. gymnopreopercularis* is more or less uniform and resembles a weak chain-link (diamond) pattern, due to distinctly dark scale margins and lighter centers (figs. 24D and 55).

Additional features useful for distinguishing *P. gymnopreopercularis* and *P. kieneri* include morphology of the infraorbital series, shape of the caudal peduncle, and development of the unpaired fins. In *P. gymnopreopercularis* the second lacrimal plate ("primitive second infraorbital" of Cichocki [1976]) is excluded from the orbit margin. Instead the anterior lacrimal plate and the third infraorbital bone in series are in contact dorsally, whereas in *P. kieneri* a narrow prong of the second lacrimal plate extends dorsally into the orbit margin, such that the anterior lacrimal plate and third infraorbital are not confluent. There is some variation with regard to degree of extension of the second lacrimal plate into the orbit margin within *P. kieneri*. The caudal peduncle is notably longer and more slender in *P. gymnopreopercularis* than in *P. kieneri*. In *P. kieneri*, the caudal margins of the soft dorsal and anal fins extend well past caudal-fin origin, even in the smallest specimens examined (figs. 36–37). In contrast, in *P. gymnopreopercularis* the caudal margins of the soft dorsal and anal fins extend only just past caudal-fin origin in the largest specimens examined (figs. 24D and 55), whereas in smaller specimens, these fin margins terminate well anterior of caudal-fin origin (fig. 56).

Paretroplus lamenabe, new species
Figures 48, 58–59; plate 1L; table 13

Paretroplus aff. *tsimoly* Mahajamba: de Rham and Nourissat, 2004: 127–129.

Paretroplus sp. "Mahajamba": Sparks and Smith, 2004: fig. 1.

HOLOTYPE: MHNG 2676.30 (ex. MHNG 2640.039), holotype, 168.5 mm SL; northwestern Madagascar: Majunga (= Mahajanga) Province: Mahajamba River at Androka (ex. MHNG 2640.039, spec. 4); J.-C. Nourissat, 23-X-2001 to 06-XI-2001.

PARATYPES: AMNH 238557, 2 ex., 165.4–167.6 mm SL; data as for holotype (ex. MHNG 2640.039, spec. 2 and 3). AMNH 238565, 2 ex., 1 ex. C&S, tissue voucher specimens, 161.2–170.5 mm SL; northwestern Madagascar: Mahajanga Province: Mahajamba River, behind Ankarafant-

Fig. 58. *Paretroplus lamenabe*, holotype, MHNG 2676.30, 168.5 mm SL; northwestern Madagascar: Mahajanga Province: Mahajamba River at Androka.

sika National Park; JSS 39-2003; J.-C. Nourissat, XI-2003. AMNH 238562, 2 ex., 178.3–181.3 mm SL; northwestern Madagascar: Majunga Province: Mahajamba River; JSS 36-2003; J.-C. Nourissat. AMNH 238566, 1 ex., 184.3 mm SL; northwestern Madagascar: Majunga Province: Mahajamba River; JSS 41-2003; J.-C. Nourissat. MHNG 2640.039, 10 ex., 161.4–183.9 mm SL; northwestern Madagascar: Majunga Province:

Fig. 59. *Paretroplus lamenabe*, paratype, AMNH 238557, 165.4 mm SL; northwestern Madagascar: Mahajanga Province: Mahajamba River at Androka.

TABLE 13

Morphometric and meristic data for *Paretroplus lamenabe*, new species. For meristics, numerals in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

		P. lamenabe			
Character	N	Holotype	Range	Mean	SD
Standard length (mm)	17	168.5	161.2–184.3	170.4	
Percentage of SL					
Head width (max.)	17	18.0	17.5–20.0	18.7	0.72
Head length	17	34.1	32.4–35.7	33.9	0.93
Body depth	17	52.7	47.0–54.3	50.1	1.87
Caudal peduncle length	17	6.3	4.9–8.3	6.5	0.79
Caudal peduncle width	17	4.5	4.4–5.9	5.0	0.43
Caudal peduncle depth	17	17.1	15.5–17.1	16.4	0.43
Pectoral-fin length	17	23.3	20.5–23.3	22.2	0.90
Pelvic-fin length	17	23.1	21.0–23.6	22.6	0.81
Pre-dorsal length	17	47.4	44.9–47.6	46.2	0.82
Pre-anal length	17	60.7	57.8–64.5	61.5	1.83
Pre-pelvic length	17	40.9	40.0–45.4	42.0	1.63
Percentage of HL					
Snout length	17	50.9	48.2–55.3	51.0	2.04
Orbit diameter	17	23.9	21.0–24.5	23.2	0.72
Upper jaw length	17	32.4	30.9–33.7	32.2	0.69
Lower jaw length	17	36.9	33.2–38.7	36.2	1.57
Interorbital width	17	37.1	30.5–37.1	33.5	1.79
Preorbital depth	17	35.4	31.7–38.5	34.3	1.64
Caudal peduncle length/width	17	1.4	1.1–1.5	1.3	0.15
Caudal peduncle length/depth	17	0.4	0.3–0.5	0.4	0.05
Scales in lateral line	17	36 (4) (H), 37 (7), 38 (4), 39 (2)			
Scales: lateral line to dorsal fin	17	6 (1), 6.5 (7), 7 (9) (H)			
Gill rakers (lower limb 1st arch)	17	12 (2), 13 (14) (H), 14 (1)			
Vertebrae (precaudal + caudal)	17	14 + 16 = 30 (1), 14 + 17 = 31 (13) (H), 15 + 16 = 31 (1), 14 + 18 = 32 (2)			
Dorsal fin	17	XV 13 (1), XV 16 (1), XVI 12 (1), XVI 13 (2), XVI 14 (1), XVII 11 (2) (H), XVII 12 (4), XVII 13 (5)			
Anal fin	17	VII 10 (1), VII 12 (1), VIII 10 (5), VIII 11 (7) (H), IX 10 (2), IX 11 (1)			

Mahajamba River at Androka; J.-C. Nourissat, 23-X-2001 to 06-XI-2001.

DIAGNOSIS: A shallow-bodied, elongate *Paretroplus* diagnosed from all congeners except *P. nourissati* and *P. tsimoly* by the presence of two wide and convergent (below the lateral midline) dark brown to black midlateral bands, representing the second and third or third and fourth bars in series. *Paretroplus lamenabe* is distinguished from *P. nourissati* and *P. tsimoly* by a deeper body (47.0%–54.3% vs. 38.1%–43.5% and 41.1%–46.8% SL in *P. nourissati* and *P. tsimoly*, respectively), by the presence of pelvic fins that extend beyond origin of the anal fin when adducted, and by a larger adult size (regularly exceeding 180 mm SL vs. less than 160 mm SL in *P. nourissati* and *P. tsimoly*).

DESCRIPTION: Morphometric and meristic data presented in table 13. Morphological characteristics and general pigmentation pattern in life and preservative can be observed in figs. 58–59. A shallow-bodied and elongate *Paretroplus* belonging to Clade F, which also includes *P. nourissati* and *P. tsimoly* (fig. 1). *Paretroplus lamenabe* is recovered as the sister taxon to a clade comprising *P. nourissati* and *P. tsimoly*, and is the largest member of this group, growing to nearly 200 mm SL. Head pointed, snout straight, and predorsal profile moderately curved. Dorsal body outline moderately curved,

ventral outline mostly straight, except posteriorly. Lips normal in development and not hypertrophied or lobed. Caudal peduncle short, deep, and laterally compressed. No readily discernable sexually dimorphic characters apparent (but see below).

Total vertebral count 30 to 32 (mode 31), with formulae of: 14 + 16, 14 + 17, 15 + 16, and 14 + 18, precaudal and caudal vertebrae, respectively.

Jaws isognathous. Lips not notably fleshy, and covered with fine papillae. Upper and lower lips not extended into median lobes or flaps (versus condition in *P. tsimoly*). Single row of spatulate unicuspid teeth in both upper and lower jaws. Teeth laterally expanded, flattened at crown, and implanted procumbently. In upper jaw, tooth on either side of premaxillary symphysis greatly enlarged, and other teeth graded in size laterally. Lower-jaw teeth at symphysis not enlarged, but reduced in size compared to adjacent lateral teeth, presumably to accommodate enlarged upper symphyseal teeth. Teeth in upper jaw number seven to nine on each side, and total 15–18. Teeth in lower jaw number three to five on each side, and total 7–10. Upper-jaw teeth relatively closely set for members of *Paretroplus*. Lower-jaw teeth irregularly and widely set.

Upper and lower pharyngeal tooth plates well developed and dentition robust. Dentition on lower pharyngeal tooth plates (= lower pharyngeal jaws [LPJ] or fifth ceratobranchial tooth plates) hooked and bicuspid both laterally and anteriorly, becoming progressively enlarged medially; robust molariform teeth present posteromedially. LPJ weakly sutured, with few weak (= shallow) interdigitations on the ventral suture, located posteroventrally. A narrow gap present between left and right fifth ceratobranchial elements posterior to ventral suture. Indentation present on ventral margin of posterior horns of LPJ. All members of Clade E exhibit both reduced number of (weak) interdigitations on ventral suture and distinct indentation on posterior horns of LPJ (Stiassny et al., 2001: 37–38, fig. 9). Six or seven robust tooth plates cover majority of dorsal surface of fourth ceratobranchial bones. Tooth plates not confluent with outer-row (= lateral) gill rakers of fourth ceratobranchial elements. Dentition on fourth ceratobranchial tooth plates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition). Dentition on third upper pharyngobranchial tooth plates molariform posteromedially, hooked and bicuspid laterally and anteromedially. Dentition on second pharyngobranchial tooth plates hooked and bicuspid, and arrayed in three rows.

Twelve to 14 triangular and elongate gill rakers arrayed along lower limb of first gill arch. Rakers denticulate dorsally and medially. All other lower-limb rakers (i.e., those on gill arches 2–4) triangular, comparatively elongate as in other members of Clade F, and strongly denticulate dorsally. On gill arches 2–4, teeth much shorter than gill-raker bases. Epibranchial rakers on first gill arch slender and elongate, and number 12 or 13. Rakers on ventral half of first epibranchial denticulate dorsomedially; those on dorsal half edentate.

Body covered with large, regularly imbricate, cycloid scales. Posterior field of lateral body scales thin and not ossified. Well-developed scale ridges (= scale sheathing) present along dorsal- and anal-fin bases. Scale ridges free from spiny dorsal and anal fins, but becoming fused to membranes of both soft dorsal and anal. On membranes between fin rays, multiple discrete rows of scales extend well beyond scale ridges and onto both soft dorsal and anal fins. Pelvic axillary scale present and well developed. Interpelvic scale elongate and rather pointed terminally. Lateral-line scales number 36–39 (mode 37). Chest scales noticeably reduced in size and embedded. Belly scales markedly reduced in size compared to chest scales, those along ventral midline smallest and very embedded. Multiple rows of scales, markedly reduced in size, extend on flanks from chest (dorsal to pelvic fins and anus) to about anal-fin origin. Four to six rows of scales on cheek. Preopercle asquamate both ventrally and along posterior margin, scaled only dorsally, and anteriorly to a varying degree, on dorsal shaft. Opercle and interopercle scaled. Snout, lacrimal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size and extending posteriorly to over 3/4 length of fin on dorsal

and ventral lobes, and 1/3 to 1/2 length of fin medially.

Dorsal with XV–XVII spines, 11–16 soft rays. Anal with VII–IX spines, 10–12 soft rays. Origin of dorsal fin located somewhat posterior to vertical through pectoral-fin insertion. Distal margins of soft dorsal and anal fins weakly produced and more or less rounded, and extend well beyond caudal-fin origin. Caudal fin weakly emarginate, upper and lower lobes broad and more or less rounded to weakly pointed. Trailing margins of upper and lower lobes weakly produced. Pectoral fin broad and rounded at distal margin. Pelvic fin extends beyond origin of anal fin when adducted. In few specimens that could reliably be sexed, caudal margins of both soft dorsal and anal fins, and caudal fin, pointed and more produced in males.

Miscellaneous Osteology and Anatomy: Large, well-developed exoccipital foramina present. Paired anterior gas bladder bullae with tough and thickened tunica externa, and anteriormost chambers firmly lodged in exoccipital recesses. Prominent excavation (= supraoccipital notch of Stiassny et al., 2001) lacking along posterior margin of supraoccipital (a single individual was found to exhibit a very shallow concavity on posterior margin of supraoccipital, but no excavation or notch). Supraoccipital extending anteriorly over median frontal pores of neurocranium (nlf_0 of Barel et al., 1977). Two distinct and well-separated proximal premaxillary-maxillary ligaments present (rostral ligament unique to *Paretroplus* within Cichlidae). An additional, fully ossified, anal- and dorsal-fin pterygiophore, not associated with any fin rays, present terminally in both fins. Nasal bones elongate. Lower pharyngeal jaw (LPJ) with reduced number of interdigitations on ventral suture and indentation on ventral face of posterior horns. Interdigitations along ventral suture of LPJ shallow and weak. Posterior horns of LPJ narrow, particularly along ventrally projecting ridges, and gap present between left and right fifth ceratobranchial elements, posterior to ventral suture.

Coloration in Life: (Based on photos and color description in de Rham and Nourissat, 2004: 127–128). Pinkish brown, grey, or bluish grey (nonbreeding, sexually quiescent) to bright yellow or orangish (presumably sexually active individual) with two prominent vertical and generally converging (below the lateral midline) brownish, dark gray, or black midlateral bars. A total of six to seven vertical bars present on flank. Apart from two prominent midlateral bars, representing the second and third or third and fourth bars in series, remaining bars generally faint, although those on posterior flank readily visible. Lips and gular region gray to light bluish grey (nonbreeding, sexually quiescent) to dark grayish blue (presumably sexually active individual). Fins dark gray (nonbreeding, sexually quiescent) to orangish yellow (presumably sexually active individual). Margins of soft dorsal and anal fins, and caudal fin, bright orange (presumably sexually active individual). Dark grey to black triangular patch generally visible in pectoral-fin axil.

Coloration in Preservative: Base body coloration gray, bluish gray, or grayish brown. Six or seven dark gray vertical bars present on flanks. Apart from two prominent midlateral bars, which generally converge below the lateral midline, remaining bars comparatively faint, although those on posterior flank readily visible (figs. 58–59). Body coloration somewhat darker overall dorsally. Dark gray to blackish triangular patch present in pectoral-fin axil. Snout, lacrimal, and interorbital region beige to dark gray. Lips pale yellow to gray. Bluish-grey to dark grayish-blue coloration on lips and gular region not evident in any preserved specimens. Unpaired fins beige, brownish gray, or charcoal gray. Posterior margins of unpaired fins light and somewhat translucent gray. Pectoral fins beige to light gray. Pelvic fins solid beige, or gray to charcoal gray with lighter gray leading edge.

Distribution and Habitats: *Paretroplus lamenabe* is known only from the lower reaches of the Mahajamba River, near the town of Androka, in northwestern Madagascar (fig. 48). De Rham and Nourissat (2004: 128) note that the Mahajamba River in this region is generally turbid and the banks muddy, but that all of the individuals were collected from a rocky stretch with an accelerated current. De Rham and Nourissat (2004) discuss a similar, and

possibly conspecific, fish that was collected from the Andranomiditra River, a tributary of the Mahajamba River, in Ankarafantsika National Park, but I have not been able to locate any preserved material for comparison. Too little is currently known regarding the distribution and abundance of *P. lamenabe* to accurately assess its conservation status.

The Mahajamba River is the next major basin to the north of the extensive Betsiboka system (fig. 48). The Mahajamba is captured by the Kamoro River, a tributary of the Betsiboka, east of Tsaramandroso and near Morafeno, such that the upper 153 km of the Mahajamba flows almost entirely into the Betsiboka basin (Aldegheri, 1972). Capture of the upper Mahajamba by the Kamoro occurs well upstream of the range of *P. lamenabe*. Moreover, in periods of low water all of the Mahajamba's water goes to the Kamoro, and from this point to the sea, the only water the Mahajamba receives is from its small tributaries (Aldegheri, 1972). Thus, the lower reaches of the Mahajamba are effectively isolated from the Kamoro and Betsiboka basins to which *P. tsimoly* is endemic (see Distribution and Habitats above for *P. tsimoly*). The isolation of the lower Mahajamba from both the upper Kamoro and Betsiboka basins may help to explain the existence of closely related yet distinct species in adjacent basins.

LOCAL NAMES: *Lamena*, *Tsimoly*, *Damba*.

ETYMOLOGY: *Lamena* is a Malagasy word that translates as "red one", and *be* is a Malagasy word meaning "big", in reference to both the live coloration of this species and its large size relative to members of its sister clade, *P. tsimoly* and *P. nourissati*.

RELATIONSHIPS AND DISCUSSION: Based on the simultaneous analysis of morphological features and nucleotide characters, *P. lamenabe* is recovered as a member of Clade F and as the sister taxon to a clade comprising *P. nourissati* and *P. tsimoly* (fig. 1). Clade F is diagnosed by two unambiguously optimized morphological transformations, the first of which is unique and unreversed: the presence of two prominent and converging midlateral bars (several fainter bars are also present on the flanks) (figs. 58–59) and elongate nasal bones. *Paretroplus damii* is recovered as the sister taxon to Clade F. Clade E, comprising *P. damii*, *P. tsimoly*, *P. nourissati*, and *P. lamenabe*, is united by five unambiguously optimized morphological features, two of which are unique and unreversed (features discussed and presented above) (fig. 1).

Interestingly, *P. nourissati*, the first member of the "lamena" group (Clade F) to be discovered, was not collected until November of 1991 (de Rham and Nourissat, 2004). The other two members of this clade, *P. tsimoly* and *P. lamenabe*, were not discovered until 1996 and 2000–2001, respectively (de Rham and Nourissat, 2004). These species are not all restricted to remote regions of the island, nor are they necessarily rare within their respective geographic ranges. For example, *P. tsimoly* was collected from the Kamilotra (= Ankalimilotrabe) River, a tributary of the Betsiboka River, just upstream from where it is crossed by the main highway between Majunga and the capital, Antananarivo (Stiassny et al., 2001; de Rham and Nourissat, 2004).

The members of Clade F are very similar morphologically. They differ primarily in body shape, development of the lips, tooth count in the oral jaws, pigmentation pattern, and coloration. Fin shape and development is also useful for distinguishing the members of this clade. In addition to greater body depth, the presence of pelvic fins that extend beyond origin of the anal fin when adducted and a larger adult size, *P. lamenabe* can generally be distinguished from *P. nourissati* and *P. tsimoly* by tooth count in the upper jaw (seven to nine on each side for a total of 15–18 vs. 13–16 and 12–14 in *P. nourissati* and *P. tsimoly*, respectively), and much more extensive squamation extending onto the soft dorsal and anal fins. No other species of *Paretroplus* has more than 16 total teeth in the upper jaw. Although Stiassny et al. (2001) report a range of 14–20 teeth in the upper jaw for *P. nourissati*, I have not been able to find a specimen with more than a total of 16 teeth.

Stiassny et al. (2001: 37–38, fig. 9) listed two features of the LPJ (= fused fifth ceratobranchial bones) that united *P. nourissati* and *P. tsimoly*, a reduced number of interdigitations on the ventral suture (poster-

oventral margin of LPJ) and an indentation on the ventral face of the posterior horns. *Paretroplus lamenabe* also shares these two LPJ features. In addition, in all three of the species comprising Clade F, the posterior horns of the LPJ are also characteristically very narrow, particularly along the ventrally projecting ridges. In addition to a reduction in number, the interdigitations along the ventral suture of the LPJ in members of Clade F are shallow and weak. All three species belonging to Clade F are also characterized by the presence of a narrow gap between the left and right fifth ceratobranchial elements, posterior to the ventral suture. This gap is most pronounced in *P. nourissati* and *P. tsimoly*, and present only at the posterior margin of the LPJ in *P. lamenabe*.

Members of Clade E, comprising Clade F and *P. damii*, also share a number of unique features related to scale morphology and squamation pattern. Uniquely in this clade, the posterior field of the lateral body scales is thin and not ossified, multiple discrete rows of scales extend onto both the soft dorsal and anal fins (figs. 58–59), the chest scales are markedly reduced in size and highly embedded, and multiple rows of scales that are markedly reduced in size extend laterally on the flank from the chest and continue posteriorly dorsal to the pelvic fin and anus, terminating at about anal-fin origin (figs. 58–59). In members of Clade F, the chest and belly scales are comparatively more reduced in size and more highly embedded than in other members of the genus, including *P. damii*. In Clade F, belly scales are so greatly reduced in size and highly embedded that the ventral chest and belly appears asquamate.

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APPENDIX 1
Comparative Material

Materials are arranged alphabetically by genus and species, with type specimens listed first followed alphabetically by museum acronym (C&S = cleared and stained preparation, S = dry skeletal preparation; number of specimens listed indicates individuals examined from each lot, and does not necessarily correspond to the total number of specimens in the lot). Locality information is provided for the Malagasy and South Asian species:

South Asian Etropline Cichlids:

Etroplus canarensis: MCZ 4316, 1 ex., possible syntype, Canara, Cannanore on Malabar Coast, Kerala, India. AMNH 217754, 1 ex., River Kumaradhara at Kalikai, southern Canara, India. AMNH 233642, 131 ex., 5 ex. C&S, Canara, India. RMNH 1103, 1 ex., Canara, India.

Etroplus maculatus: AMNH 37930, 1 ex., India. AMNH 215904, 7 ex. C&S, aquarium specimens, no locality data. AMNH 217755, 4 ex., India. AMNH 217758, 14 ex., Sri Lanka. FMNH 58986, 2 ex., Colombo, Sri Lanka. FMNH 76016, 37 ex., 2 ex. C&S, India. MCZ 4311, 1 ex., Kerala, Laccadive Sea, Canara, Cannanore on Malabar Coast, India. USNM 301168, 6 ex., 2 ex. C&S, near Negombo Point, Sri Lanka.

Etroplus suratensis: AMNH 217756, 1 ex., District Salem T.V., Mettur Dam Reservoir, Madras, India. AMNH 217757, 32 ex., 7 ex. C&S, Negombo Lagoon, Sri Lanka. FMNH 58987, 8 ex., Colombo, Sri Lanka. MCZ 4306, 2 ex., Kerala, Laccadive Sea, Canara, Cannanore on Malabar Coast, India. USNM 301178, 6 ex., 2 ex. C&S, near Negombo Point, Sri Lanka.

Malagasy Ptychochromine Cichlids:

Katria katria: AMNH 217739, holotype, eastern Madagascar, Tamatave Province, River Nosivolo, below Zule's Village, large side pool off main stream. AMNH 217740, 8 ex., paratypes, eastern Madagascar, Tamatave province, River Nosivolo, below Ampasimaniona village, 26 kilometers east-northeast of Marolambo. AMNH 93701, 20 ex., 10 ex. C&S, eastern Madagascar, Tamatave Province, River Nosivolo below Ampasimaniona Village, 26 km east-northeast of Marolambo. UMMZ uncat., 5 ex., 1 ex. C&S, eastern Madagascar, Tamatave Province, Mangoro drainage, Nosivolo River, near Marolambo.

Oxylapia polli: MNHN 1965-317, 1 ex., syntype. AMNH 97098, 1 ex. AMNH 97111, 10 ex., 1 ex. C&S. MNHN 1966-1034, 2 ex., 1 ex. C&S. UMMZ 235046, 2 ex., 1 ex. C&S. All from Madagascar, Tamatave Province, Mangoro drainage, village of Marolambo, Nosivolo River.

Paratilapia bleekeri: MNHN A-4195, 3 ex., syntypes. MNHN A-4196, 1 ex., syntype. All from Madagascar, central highlands, near Antananarivo.

Paratilapia polleni: RMNH 3.934, 2 ex., syntypes, island of Nosy Be, Madagascar. RMNH 4.483, 1 ex., syntype, Madagascar. RMNH 6.690, 2 ex., syntypes, "Ambassuana, Madagascar septentrionalis, in fluvis". UMMZ 235043, 42 ex., 2 ex. C&S, Lac Anjavibe, island of Nosy Be, Madagascar. UMMZ 239552, 8 ex., Lac de Deux Soures, island of Nosy Be, Madagascar.

Paratilapia typus: RMNH 6692, holotype, eastern Madagascar. AMNH uncat., 5 ex., Tamatave Province, Mananara River.

Paratilapia cf. *bleekeri*: UMMZ 235044, 7 ex., Vahifito River, near Vevembe, southeastern Madagascar. UMMZ 235045, 2 ex. C&S, Sahapindra River, near Vevembe, southeastern Madagascar. UMMZ 238478, 17 ex., Mananjary, southeastern Madagascar. UMMZ 239551, 1 ex., north of Karianga at town of Mahavelo, Andriambondro River, southeastern Madagascar. UMMZ 239557, 2 ex., Manombo Special Reserve, south of Farafangana, southeastern Madagascar. UMMZ 239564, 1 ex., Ampijoroa Forestry Station, Lake Ravelobe, northwestern Madagascar. UMMZ 240359, 3 ex. C&S, rivers near Vevembe camp, southeastern Madagascar. UMMZ 244626, 5 ex., Vahifito River, west of Vevembe camp, southeastern Madagascar.

Ptychochromoides betsileanus: BMNH 1882.2.25: 69, lectotype, Betsileo, Madagascar. BMNH 1882.2.25:70, 1 ex., paralectotype, Betsileo, Madagascar. BMNH 1909.7.27:53, 1 ex., originally from Paris Museum, no locality information. AMNH 217753, 1 ex., Ilanana River, near Ranohira, Onilahy drainage, Madagascar. AMNH 217763, 1 ex., Manantanana River, headwaters near Iaritsena, Ambalavao Region, Mangoky drainage, Madagascar. MNHN 1907-0104, 2 ex., Madagascar. MNHN 1960-255, 1 ex., Madagascar. MNHN 1965-314, 1 ex., Ambalavao, south-central Madagascar. UMMZ 238114, 3 ex., Madagascar. UMMZ 238115, 5 ex. S, Ilanana River,

south of Isalo National Park, south-central Madagascar.

Ptychochromoides itasy: UMMZ 243393, holotype, Madagascar. AMNH 233643, 1 ex., paratype, Madagascar. MNHN 1919-11, 1 ex. C&S, Madagascar, central highlands, Region of Antananarivo, Lake Itasy. UMMZ 199409, 1 ex., Madagascar.

Ptychochromoides vondrozo: UMMZ 235297, holotype, Madagascar, Fianarantsoa Province, Region of Vondrozo, near village of Vevembe, Mananara drainage basin, Ramanara River, tributary of Sahampindra River, 22°48′51.5″S, 47°08′28.7″E, alt. 518 m. Paratypes: All localities in Madagascar: Fianarantsoa Province: Region of Vondrozo, near village of Vevembe: Mananara drainage basin: AMNH 228488, 2 ex., same data as for holotype. UAZ 2000-1-1, 1 ex., same data as for holotype. UMMZ 235293, 1 ex., Sahampindra River, 22°48′20.3″S, 47°09′21.7″E. UMMZ 235294, 3 ex., 1 ex. C&S, Sahampindra River, approx. 10 km upstream from Vevembe Camp, 22°49′38.9″S, 47°07′41.1″E, alt. 427 m. UMMZ 235295, 1 ex., Voatavobe River, tributary of Vahafito River. UMMZ 235296, 3 ex., same data as for holotype.

Ptychochromis curvidens: MHNG 2623.82, holotype, northern Madagascar, Antsiranana (Diego Suarez) Province, Andranofanjava, Andranofanjava-Sandriapiana River system, P. de Rham and J.-C. Nourissat, 9 Oct., 1999. MHNG 2676.096, 2 ex., paratypes, data as for holotype. AMNH 237133, 2 ex., 1 ex. C&S, paratypes, data as for holotype. MHNG 2623.84, 1 ex., paratype, northern Madagascar, Antsiranana (Diego Suarez) Province, Mirosolava, P. de Rham and J.-C. Nourissat, 10 Oct., 1999.

Ptychochromis grandidieri: MNHN A.4147, holotype, Madagascar, region of high forests. AMNH 88018, 56 ex., 1 ex., C&S, southeastern Madagascar, Mananjary, estuary of Mananjary River, 21°05′S, 48°27′E. AMNH 88053, 2 ex., southeastern Madagascar, Mananjary, estuary of Mananjary River, 21°05′S, 48°27′E. AMNH 88076, 2 ex., eastern Madagascar, Vatomandry, 19°20′S, 49°00′E. AMNH 88090, 3 ex., eastern Madagascar, Mahanoro, 19°55′S, 48°50′E. AMNH 88092, 17 ex., eastern Madagascar, Mahanoro, Pangalanes canal north of Mangoro River. AMNH 88102, 36 ex., 14 ex. C&S, eastern Madagascar, bay lake behind dunes, c. 100 m from sea. AMNH 88117, 18 ex., eastern Madagascar, Tamatave market, 18°10′S, 49°25′E. AMNH 88140, 1 ex., eastern Madagascar, 25 km north of Tamatave, Pangalanes canal, 18°00′S, 49°25′E. AMNH 88153, 11 ex., eastern Madagascar, between Fenerive and Tamatave, Pangalanes canal, 18°00′S, 49°25′E. AMNH 96999, 52 ex., 2 ex. C&S, eastern Madagascar, Tamatave Province, Mangoro River near mouth. AMNH 97008, 185 ex., eastern Madagascar, Salehy village, 1 km south of turnoff from Marolambo-Mananjary road, 19°55′S, 48°50′E. AMNH 97012, 12 ex., eastern Madagascar, Mahanoro market. AMNH 97028, 7 ex., 3 ex. C&S, eastern Madagascar, Tamatave Province, bay lake behind first dune ca. 100 m from sea, east of road by Sahey Village, 1 km south of turnoff from Marolambo-Manajary Road. AMNH 97057, 1 ex., eastern Madagascar, Ambodisovoka village, Savalany River. AMNH 228067, 3 ex., southeastern Madagascar, Lopary, Mananizo River. AMNH 228072, 6 ex., southeastern Madagascar, Ampataka village, Sahambavy River. AMNH 228074, 3 ex., southeastern Madagascar, 12 km north of Farafangana, Manampatrona River, 22°43′47″S, 47°47′25″E. AMNH 231347, 1 ex., southeastern Madagascar, Ampataka village, Sahambavy River, 23°21′04″S, 47°28′18″E. AMNH 231352, 4 ex., southeastern Madagascar: Manombo Special Reserve, Takoandra River, 23°01′27″S, 47°43′16″E. MNHN A.310, 1 ex., rivers that cross the eastern slope, Lantz. MNHN A.7896, 2 ex., central Madagascar to the west of Antananarivo, Lac Itasy(?). MNHN 1901-0020, 1 ex., eastern Madagascar, Tamatave. MNHN 1901-0021, 1 ex., eastern Madagascar, Tamatave. MNHN 1932-0082, 1 ex., eastern Madagascar, Manompana. MNHN 1932-0083, 13 ex., eastern Madagascar, Manompana. MNHN 1935-0007, 1 ex., eastern Madagascar, Mananara. UMMZ 233524, 17 ex., 2 ex. C&S, Madagascar, southeastern coastal region. UMMZ 237311, 22 ex., southeastern Madagascar, Mananjary. UMMZ 237312, 3 ex., 1 ex. C&S, southeastern Madagascar, Manombo Special Reserve. UMMZ 237495, 5 ex., southeastern Madagascar, 6 km north of Karianga at Mahavelo, Rienana drainage, Andriambondro River, 22°21′47″S, 47°22′05″E. UMMZ 238453, 2 ex., southeastern Madagascar, near Manombo Special Reserve. UMMZ 238471, 1 ex., southeastern Madagascar, Mananjary port. UMMZ 238472, 11 ex., 2 ex. C&S, southeastern Madagascar, Farafangana market. UMMZ 238476, 7 ex., Madagascar, southeastern coastal region.

Ptychochromis inornatus: UMMZ 237492, holotype, northwestern Madagascar, Antalaha Province, northeast of Antsohihy, Ankofia drainage, Anjingo River, 14°50′41.0″S, 48°14′38.3″E. UMMZ 237063, 5 ex., 1 ex. C&S, paratypes, data as for holotype. AMNH 230746, 2 ex., paratypes, data as for holotype. UMMZ 237064, 5 ex., 2 ex. C&S, paratypes, northwestern Madagascar, Antalaha Province, northeast of Antsohihy, Ankofia drainage, Bora Special Reserve, Bemahavony River (tributary of Anjingo River, 14°52′20.4″S, 48°14′52.2″E. AMNH 230747, 2 ex., paratypes, data as for UMMZ 237064. UMMZ 237065, 1 ex., paratype, northwestern Madagascar, Antalaha Province, northeast of Antsohihy, Ankofia drainage, Lake Andrapongy, 14°41′49.3″S, 48°07′54.3″E. UMMZ 237067, 7 ex., paratypes, northwestern Madagascar, Antalaha Province, northeast of Antsohihy, Ankofia drainage, Anjingo River, 14°50′39.7″S, 48°14′39.5″E.

Ptychochromis insolitus: UMMZ 237066, holotype, northeastern Madagascar, Mahajanga Province, near town of Mandritsara, Sofia drainage basin, Amboaboa River, 15°50′1″S, 48°42′51″E, J. S. Sparks and K. J. Riseng, 10 July 1996. AMNH 237134, 2 ex., aquarium-raised specimens, northwestern Madagascar, purportedly offspring of specimens collected in Mangarahara River, Sofia River drainage basin.

Ptychochromis loisellei: AMNH 232462, holotype, northeastern Madagascar, Antsiranana Province, north of Sambava, Mahanara River at Antsirabe-Nord, just upstream of bridge over route N-5, 13°58′29.4″S, 49°57′48.6″E, P. V. Loiselle and local fishermen, 1 Nov., 2001. AMNH 231249, 1 ex., paratype, northeastern Madagascar, Antsiranana Province, main channel of the Mahanara River at Antsirabe-Nord, at bridge on Route N-5, 13°38′29.4″S, 49°57′48.6″E, P. V. Loiselle, 9 Oct., 2000. AMNH 231258, 3 ex., 1 ex. C&S, paratypes, northeastern Madagascar, Antsiranana Province, main channel of the Mahanara River at Antsirsabe-Nord, at bridge on Route N-5, 13°58′29.4″S, 49°57′48.6″E, P. V. Loiselle, 13 Oct., 2000. MNHN 2006-0781, 1 ex., paratype, data as for AMNH 231258. AMNH 232458, 1 ex., paratype, northeastern Madagascar, Antsiranana Province, Mahanara River, ca. 4 km northwest of Antsirabe-Nord, 13°57′18.0″S, 49°56′12.0″E, P. V. Loiselle and local fishermen, 31 Oct., 2001. MHNG 2676.095, 1 ex., paratype, data as for AMNH 232458. AMNH 237135, 5 ex., paratypes, data as for holotype.

Ptychochromis makira: AMNH 237131, holotype, northeastern Madagascar, Toamasina Province, north of Maroansetra, near town of Marovonona, Antainambalana River, purchased from local fishermen, A. Sarovy, J. S. Sparks, W. L. Smith, and K. L. Tang, Nov. 2003. AMNH 237132, 1 ex. (C&S in part), paratype, data as for holotype.

Ptychochromis oligacanthus: RMNH 3.936, lectotype; "Madagascar, in flumine Samberano, Nossibé, in lacu Pambilao", Pollen and van Dam. AMNH 18841, 1 ex., Madagascar, probably mainland, Sambirano region. AMNH 58491, 9 ex., northwestern Madagascar, Lake Amparihibe, at the mouth of the inflowing small stream, Lake Antsidihy, Nosy Be. AMNH 215522, 4 ex., northwestern Madagascar, Lake Bemapaza, Nosy Be. AMNH 215523, 15 ex., northwestern Madagascar, Lakes Djabala and Ampombilava, Nosy Be. AMNH 230699, 3 ex., northwestern Madagascar, Lake Andjavibe, Nosy Be. AMNH 232399, 2 ex., northwestern Madagascar, Lake Ampombilava, Nosy Be. AMNH 232415, 3 ex., northwestern Madagascar, Lake Djabala, Nosy Be. MNHN 1962-322, 1 ex., northwestern Madagascar, Sambirano River. UMMZ 236591, 26 ex., 4 ex. C&S, northwestern Madagascar, Lake Ampombilava, Nosy Be. UMMZ 237498, 22 ex., 2 ex. C&S, northwestern Madagascar, Lake Djabala, Nosy Be. UMMZ 237493, 3 ex., northwestern Madagascar, Lac de Deux Soeurs, Nosy Be. UMMZ 237494, 1 ex., northwestern Madagascar, Lake Amparihibe, Nosy Be. UMMZ 237496, 6 ex., northwestern Madagascar, Lake Bempazava, Nosy Be. UMMZ 237497, 8 ex., northwestern Madagascar, Lake Anjavibe, Nosy Be. UMMZ 237499, 11 ex., 1 ex. C&S, northwestern Madagascar, Mananjeba drainage, Andranomaloto River, northeast of town of Ambanja.

Ptychochromis onilahy: MNHN 1962-0201, holotype, southwestern Madagascar, Province of Tulear, Onilahy River, A. Kiener. AMNH 237130, 1 ex. (C&S in part), paratype, data as for holotype. MNHN 2006-0780, 3 ex., paratypes, data as for holotype.

AFRICAN CICHLIDS:

Aulonocranus dewindti: UMMZ 199865, 151 ex., 2 ex. C&S.

Chromidotilapia guentheri: UMMZ 195047, 28 ex., 1 ex. C&S. USNM 304030, 5 ex.
Haplochromis bloyeti (strigigena): UMMZ 166637, 324 ex., 4 ex. C&S.
Haplochromis brownae: UMMZ 187374, 5 ex., 1 ex. C&S.
Haplochromis n. sp. "silver bullet": UMMZ uncat., 10 ex., 2 ex. C&S.
Hemichromis bimaculatus: UMMZ 195049, 2 ex. C&S. UMMZ 199390, 1 ex. C&S. UMMZ 146263, 3 ex. UMMZ 218788, 16 ex. UMMZ 169018, 10 ex. UMMZ 218790, 4 ex.
Hemichromis fasciatus: UMMZ 196187-S, 1 ex. S. UMMZ 187906, 77 ex.
Heterochromis multidens: BMNH 1921.12.21.78, 1 ex., possible type. AMNH 5963, 1 ex. AMNH 5963 SW, 1 ex. C&S. AMNH 216062, 1 ex. C&S. CU 89065, 1 ex. CU 88258, 8 ex. NRM 37024, 1 ex. CS. MRAC 46179, 1 ex. MRAC 7779-7780, 2 ex. MRAC 60893, 1 ex. C&S. MRAC 167929, 1 ex. MRAC 61914-61915, 2 ex. MRAC 63239, 1 ex. MRAC 73-23-P-6720-721, 2 ex. MRAC 167924-928, 5 ex., 1 ex. C&S.
Neolamprologus brichardi: UMMZ 196135, 7 ex., 1 ex. C&S. UMMZ 196162, 12 ex.
Neoamprologus tetracanthus: UMMZ 201596-S, 2 ex. S.
Oreochromis mossambicus: UMMZ 203324, 2 ex. C&S. UMMZ 199401-S, 1 ex. S. UMMZ 189143, 8 ex. UMMZ 189175, 5 ex.
Pseudocrenilabrus philander: UMMZ 200025, 4 ex. C&S. UMMZ 200351, 139 ex., 3 ex. C&S.
Pseudotropheus (Metriaclima) zebra: UMMZ 218362, 16 ex., 2 ex. C&S. UMMZ uncat., 2 ex. S.
Pseudotropheus macropthalmus: UMMZ 218360, 3 ex.
Serranochromis macrocephalus: UMMZ 200095-S, 1 ex. S. UMMZ 200096-S, 1 ex. S. UMMZ 200113-S, 2 ex. S. UMMZ 200127-S, 1 ex. S. UMMZ 200048, 9 ex. UMMZ 200284, 2 ex. UMMZ 218428, 33 ex., 2 ex. C&S.
Tilapia rendalli: UMMZ 200115-S, 4 ex. S. UMMZ 200289, 3 ex. C&S. UMMZ 200196, 33 ex.
Tropheus moorei: UMMZ 199956, 71 ex., 2 ex. C&S.
Tylochromis bangwelensis: UMMZ 200198, 8 ex., 1 ex. C&S.
Tylochromis lateralis: AMNH 58041 SW, 1 ex. C&S.
Tylochromis mylodon: UMMZ 200400, 1 ex.
Tylochromis polylepis: AMNH 216056 SW, 1 ex. C&S. UMMZ 196072, 1 ex. UMMZ 196073, 2 ex.

NEOTROPICAL CICHLIDS:

Acaronia nassa: UMMZ 215945, 1 ex. C&S. UMMZ 204541, 1 ex. C&S. UMMZ 215929, 2 ex. S. UMMZ 215930, 1 ex. S. UMMZ 224185, 13 ex. UMMZ 224759, 2 ex. UMMZ 215955, 1 ex. UMMZ 224195, 1 ex. UMMZ 216516, 1 ex.
Archocentrus (Cichlasoma) nigrofasciatus: UMMZ 199383, 1 ex. C&S. UMMZ 181823, 19 ex. UMMZ 197392, 23 ex. UMMZ 194157, 3 ex. C&S. UMMZ 190788, 5 ex.
Astronotus ocellatus: UMMZ 199378, 1 ex. C&S. UMMZ 199731, 1 ex. UMMZ 207255, 2 ex. S. UMMZ 179614, 1 ex. UMMZ 204579, 1 ex. UMMZ 204644, 4 ex. UMMZ 216904, 1 ex. USNM 344762, 5 ex., 1 ex. C&S. USNM 329639, 5 ex., 1 ex. C&S.
Bujurquina (Aequidens) vittata: UMMZ 207269, 2 ex. C&S. UMMZ 207845-S, 7 ex. S. UMMZ 216655, 2 ex. UMMZ 207845, 13 ex. UMMZ 208125, 6 ex.
Chaetobranchopsis australis: UMMZ 207256, 11 ex., 3 ex. C&S. UMMZ 207906, 1 ex. UMMZ 205893, 3 ex. UMMZ 208128, 4 ex.
Cichla ocellaris: UMMZ 216098, 1 ex. C&S. UMMZ 215716, 1 ex. C&S. UMMZ 215952, 3 ex. C&S. UMMZ 215948, 1 ex. C&S. UMMZ 204679-S, 3 ex. S. UMMZ 204407-S, 1 ex. S. UMMZ 215931, 1 ex. S. UMMZ 147358, 1 ex. UMMZ 215543, 26 ex. UMMZ 216517, 1 ex. UMMZ 214789, 1 ex. UMMZ 204978, 1 ex.
Cichla temensis: UMMZ 215931, 1 ex. S.
Cichlasoma bimaculatum: UMMZ 203468, 168 ex., 2 ex. C&S. UMMZ 199736-S, 1 ex. S. UMMZ 206705-S, 2 ex. S. UMMZ 215934, 2 ex. S. UMMZ 206994, 11 ex. S. UMMZ 205110, 13 ex. UMMZ 205925, 5 ex.
Crenicichla saxatilis: UMMZ 147381, 1 ex. C&S. UMMZ 204938, 1 ex. C&S. UMMZ 215914, 9 ex., 1 ex. C&S. UMMZ 215935, 5 ex. S. UMMZ 215958, 1 ex. UMMZ 204938, 7 ex.
Geophagus surinamensis: UMMZ 215721, 2 ex. C&S. UMMZ 215933-S, 2 ex. S. UMMZ 204939, 15 ex. UMMZ 204939-S, 3 ex. S. UMMZ 204527-S, 1 ex. S. UMMZ 204242, 65 ex. UMMZ 204480, 29 ex.
Gymnogeophagus setequedas: UMMZ 206457, 53 ex., 2 ex. C&S, 1 ex. S. UMMZ 206916, 18 ex.
Parachromis managuensis: UMMZ 197401, 2 ex. C&S. UMMZ 199603-S, 1 ex. S. UMMZ 230831-S, 1 ex. S. UMMZ 223246-S, 1 ex. S. UMMZ 197347, 3 ex. UMMZ 199603, 26 ex.
Petenia splendida: UMMZ 196665, 37 ex., 2 ex. C&S. UMMZ 205457-S, 1 ex. S. UMMZ

189987-S, 2 ex. S. UMMZ 223251, 1 ex. S. UMMZ 196254, 1 ex. S. UMMZ 188028-S, 1 ex. S. UMMZ 144103, 8 ex.
Pterophyllum scalare: AMNH 15480 SW, 1 ex. C&S. UMMZ 2033481, 3 ex. UMMZ 216088, 1 ex. UMMZ 235778, 18 ex.
Pterophyllum eimaki: UMMZ 162860, 2 ex. C&S.
Retroculus lapidifer: AMNH uncat., 2 ex., 1 ex. C&S. MNRJ 12910, 10 ex.
Satanoperca jurupari: UMMZ 215936, 1 ex. C&S. UMMZ 216421, 2 ex. C&S. UMMZ 216520, 2 ex. UMMZ 205158, 9 ex. UMMZ 204581, 34 ex. UMMZ 204615, 16 ex.
Symphysodon aequifasciatus: USNM 103854, 2 ex., 1 ex. C&S. USNM 191597, 7 ex.
Symphysodon discus: UMMZ 182551-S, 2 ex. S. UMMZ 179617-S, 1 ex. S. UMMZ 186200-S, 1 ex. S.
Teleocichla cinderella: MNRJ 13943, 10 ex., 1 ex. C&S.
Teleocichla sp.: MNRJ 14848, 10 ex.
Vieja synspila: UMMZ 196577, 2 ex. C&S. UMMZ 188029-S, 3 ex. S. UMMZ 210901, 16 ex. UMMZ 144056, 33 ex.

NONCICHLIDS:

Centrarchidae:
Micropterus salmoides: UMMZ 193674, 2 ex. C&S. UMMZ 114607-S, 1 ex. S. UMMZ 182062-S, 1 ex. C&S. UMMZ 179967-S, 1 ex. C&S. UMMZ 105982-S, 1 ex. C&S. UMMZ 189874-S, 1 ex. C&S.
Embiotocidae:
Taeniotoca lateralis: UMMZ 92700, 2 ex. C&S. UMMZ 92703, 34 ex.
Embiotoca jacksoni: UMMZ 142377, 2 ex. C&S. UMMZ 179924, 1 ex. S. UMMZ 92598, 2 ex.
Haemulidae:
Haemulon aurolineatum: UMMZ 172380, 2 ex. C&S. UMMZ 179125-S, 1 ex. S. UMMZ 181672, 1 ex. S. UMMZ 174047, 8 ex.
Pomadasys maculatus: UMMZ 226971, 1 ex. C&S.
Labridae:
Halichoeres bivittatus: UMMZ 147781, 2 ex. C&S. UMMZ 187840, 1 ex. S. UMMZ 172385, 11 ex.
Halichoeres radiatus: UMMZ 154038, 2 ex. UMMZ 186991-S, 1 ex. S. UMMZ 173410-S, 1 ex. S.
Thalassoma bifasciatum: UMMZ 174180, 2 ex. C&S.
Lutjanidae:
Lutjanus vitta: UMMZ 227039, 2 ex. C&S. UMMZ 220023, 3 ex.
Lutjanus griseus: UMMZ 187084, 1 ex. S.
Pomacentridae:
Abudefduf saxatilis: UMMZ 189794, 2 ex. C&S. UMMZ 234189, 2 ex. UMMZ 185577, 8 ex. UMMZ 187048-S, 2 ex. S. UMMZ 187072-S, 2 ex. C&S. UMMZ 186990-S, 1 ex. S.
Chromis opercularis: UMMZ 185581, 1 ex. C&S.
Scaridae:
Scarus croicensis: UMMZ 176546, 1 ex. C&S.
Scarus guacamaia: UMMZ 187010-S, 1 ex. S. UMMZ 186951-S, 1 ex. S.
Serranidae:
Serranus fasciatus: UMMZ 190287, 1 ex. C&S. UMMZ 190287, 9 ex.
Serranus subligarius: UMMZ 189185-S, 1 ex. S.
Cephalopholis boenak: UMMZ 182741, 1 ex. C&S. UMMZ 182741, 10 ex. UMMZ 234188, 5 ex.
Cephalopholis (*Epinephelus*) *fulvus*: UMMZ 173404-S, 2 ex. S.
Epinephelus nigritus: UMMZ 187057, 1 ex. S.
Epinephelus striatus: UMMZ 172556-S, 1 ex. S.
Sparidae:
Lagodon rhomboides: UMMZ 136340, 2 ex. C&S. UMMZ 179129-S, 2 ex. S. UMMZ 186960-S, 1 ex. S. UMMZ 189182-S, 2 ex. S. 181669-S, 1 ex. S. UMMZ 139290, 16 ex.

APPENDIX 2

Morphological Character Matrix

Characters correspond numerically to those listed in the Results. Missing data are coded as "?" and inapplicable character assignments are indicated by "-". See Methods for a discussion of character coding. Characters (total = 82) are arranged sequentially in rows and numbered from left to right (i.e., row 1 = characters 1–11, row 2 = characters 12–22, etc.).

Retroculus lapidifer

0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 1 0
0 0 1 1 0 0 0 0 0 0 0
0 0 0 1 0 0 0 0 1 0 0
0 0 0 0 0 0 0 - 0 0 0
0 0 - - - - - 0 0 0 0
0 - 0 0 0 1 1 0 0 1 0
0 0 0 0 0

Heterochromis multidens

0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0
0 1 0 - - 0 0 0 0 0 0
0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 - 0 0 0
0 1 0 - - 0 0 0 1 0 0
0 - 0 0 0 1 1 0 0 0 0
0 0 0 0 0

Ptychochromis grandidieri

1 1 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1
0 1 2 0 1 1 1 1 0 0 0
0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 - 0 1 1
0 1 1 0 - 0 0 0 1 0 0
0 - 0 0 0 0 0 0 0 0 0
0 0 0 0 0

Ptychochromis oligacanthus

1 1 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1
0 1 2 0 1 0 0 1 0 0 0
0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 - 0 1 1
0 1 1 0 - 0 0 0 1 0 0
0 - 0 0 0 0 0 0 0 0 0
0 0 0 0 0

Ptychochromoides vondrozo

1 1 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0
0 1 2 0 1 1 1 1 0 0 0
0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 - 0 1 1
0 1 1 0 - 0 0 0 0 0 0
0 - 0 0 0 0 1 0 0 0 0
1 0 0 1 0

APPENDIX 2
(Continued)

Katria katria

1	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	1	2	0	1	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	-	0	1	1
0	1	0	0	-	0	0	0	1	0	0
0	-	0	0	0	0	0	0	0	0	0
0	0	0	0	0						

Oxylapia polli

1	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	1	0	0	0
0	1	1	1	1	0	0	1	0	0	1
0	0	0	0	0	0	0	0	0	0	0&1
0	0	0	0	0	0	0	-	0	1	1
0	1	0	0	-	0	0	0	0	0	0
0	-	0	0	0	0	1	0	0	0	0
1	0	0	0	0						

Paratilapia cf. *bleekeri*

0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	-	-	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	-	0	0	0
0	1	1	1	0	0	0	0	0	0	0
0	-	0	0	0	0	0	0	0	0	0
0	0	1	0	0						

Paratilapia polleni

0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	-	-	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	-	0	0	0
0	1	1	1	0	0	0	0	0	0	0
0	-	0	0	0	0	0	0	0	0	0
0	0	1	0	0						

Etroplus canarensis

1	0	0	1	0	0	0	1	0	1	1
1	1	1	1	1	1	1	1	1	0	0
0	0	1	1	1	1	1	0	1	1	0
1	1	1	0	1	-	0	1	0	1	0
1	1	1	1	1	1	1	0	1	0	0
2	1	1	1	1	0	0	1	0	1	0
1	0	1	0	1	0	0	0	0	1	0
0	0	0	1	1						

APPENDIX 2
(Continued)

Etroplus maculatus

1	0	0	1	0	0	0	1	0	1	1
1	1	1	1	1	1	1	1	1	0	0
0	0	2	1	1	1	1	0	1	1	0
1	1	1	0	0	-	0	1	0	1	0
1	1	1	1	1	1	1	0	1	0	0
2	1	1	1	1	0	0	1	0	0	0
1	0	1	0	1	0	0	0	0	0	0
0	0	0	0	0						

Etroplus suratensis

1	0	0	1	0	0	0	1	0	1	1
1	1	1	1	1	1	1	1	1	0	0
0	0	2	1	1	1	1	0	1	1	0
1	1	1	0	1	-	0	1	0	1	0
1	1	1	1	1	1	1	0	1	0	0
2	1	1	1	1	0	0	1	0	1	0
1	0	1	0	1	0	0	0	0	1	0
0	0	0	0	1						

Paretroplus damii

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	1	1	1	1	1	0	0	0
0	0	0	1	0						

Paretroplus dambabe

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	1	1
1	1	1	0	1	0	0	0	1	1	0
0	0	0	0	0						

Paretroplus gymnopreopercularis

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	0	1	0	0	0	0	0	0
0	1	0	0	0						

APPENDIX 2
(Continued)

Paretroplus kieneri (Betsiboka River)

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	0	1	0	0	0	0	0	0
0	1	0	0	0						

Paretroplus kieneri (Lake Kinkony: topotypic)

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	0	1	0	0	0	0	0	0
0	1	0	0	0						

Paretroplus lamenabe

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	1	1	1	1	1	0	0	1
0	0	0	1	0						

Paretroplus maculatus

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	1	1
1	1	1	0	1	0	0	0	1	1	0
0	0	0	0	0						

Paretroplus maromandia

1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	1	1
1	1	1	0	1	0	0	0	1	1	0
0	0	0	0	0						

APPENDIX 2
(Continued)

Paretroplus menarambo										
1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	2	0	0	0
1	1	1	1	1	1	1	1	0	1	1
1	1	1	0	1	0	0	0	1	1	0
0	0	0	0	0						
Paretroplus nourissati										
1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	1
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	1	1	1	1	1	0	0	1
0	0	0	1	0						
Paretroplus petiti (holotype)										
1	0	1	0	1	1	1	1	1	?	?
?	1	1	1	2	1	1	1	1	0	?
?	?	?	?	?	1	1	?	?	?	1
?	?	0	1	1	1	?	?	?	?	?
1	1	1	1	1	1	1	?	0	0	0
1	1	1	1	1	1	?	1	0	1	1
1	1	1	0	1	0	0	0	1	?	0
0	0	0	0	0						
Paretroplus polyactis										
1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	2	1	1	1	1	0	0
1	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1&2	0	0	0
1	1	1	1	1	1	1	1	0	0	1
1	1	1	0	1	0	0	0	0	1	0
0	0	0	0	0						
Paretroplus tsimoly										
1	0	1	0	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	1	1	0
?	0	2	1	1	1	1	1	1	1	1
1	1	0	1	1	1	1	1	1	1	1
1	1	1	1	1	1	1	1	0	0	0
1	1	1	1	1	1	1	1	0	0	0
1	0	1	1	1	1	1	1	0	0	1
0	0	0	1	0						

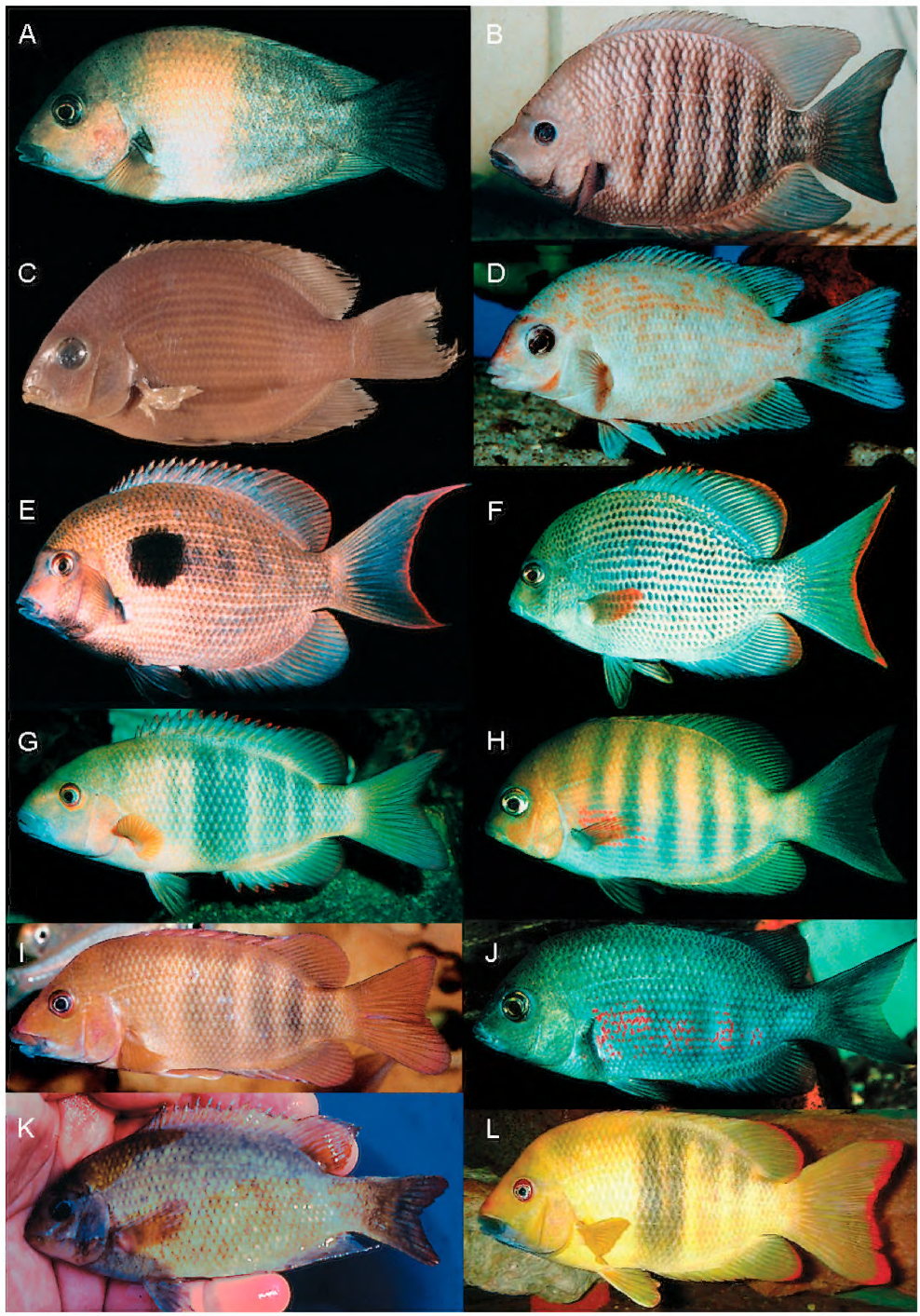

Plate 1. Live coloration of species of *Paretroplus* (except *P. petiti*, known only from formalin-fixed holotype): **A,** *P. damii*. **B,** *P. polyactis*. **C,** *P. petiti*. **D,** *P. kieneri*. **E,** *P. maculatus*. **F,** *P. menarambo*. **G,** *P. nourissati*. **H,** *P. maromandia*. **I,** *P. tsimoly*. **J,** *P. dambabe*. **K,** *P. gymnopreopercularis*. **L,** *P. lamenabe*. Photos A, B, and D–J by Paul Loiselle. Photo K by Jean Claude Nourissat. Photo L by Dave Tourle.